

BULLETIN

OF

THE NEW YORK STATE COLLEGE OF FORESTRY
AT SYRACUSE UNIVERSITY
HUGH P. BAKER, *Dean*

Roosevelt Wild Life Bulletin

VOLUME 5

NUMBER 4

OF THE

Roosevelt Wild Life Forest Experiment Station



THE BIOLOGY OF THE VOLES OF NEW YORK

THE RELATION OF MAMMALS TO THE
HARVARD FOREST

CONTENTS OF RECENT ROOSEVELT WILD LIFE BULLETINS

(To obtain these publications see announcement on back of title page.)

ROOSEVELT WILD LIFE BULLETIN, Vol. 1, No. 3. March, 1923.

1. The Summer Birds of the Allegany State Park....Aretas A. Saunders.
2. The Ruffed Grouse, with Special Reference to its Drumming.....
Edmund J. Sawyer.
3. Current Station Notes.....The Director and Editor.

ROOSEVELT WILD LIFE BULLETIN, Vol. 1, No. 4. March, 1923.

1. Relation of Summer Birds to the Western Adirondack Forest.....
Perley M. Silloway.
2. Notes on the Relation of Birds to Adirondack Forest Vegetation.....
Dr. Charles C. Adams.
3. The Summer Birds of the Adirondacks in Franklin County, N. Y.....
Theodore Roosevelt, Jr., and H. D. Minot.
(Reprinted: original date of publication, 1877.)
4. Current Station Notes.....The Director and Editor.

ROOSEVELT WILD LIFE BULLETIN, Vol. 2, No. 1. October, 1923.

1. The Control of Blood-sucking Leeches, with an Account of the Leeches
of Palisades Interstate Park.....Dr. J. Percy Moore.
2. Preliminary Report on the Parasitic Worms of Oneida Lake, New
York.....Dr. Henry S. Pratt.
3. Acanthocephala from the Fishes of Oneida Lake, New York.....
Dr. Harley J. Van Cleave.
4. Current Station Notes.....The Director and Editor.

ROOSEVELT WILD LIFE BULLETIN, Vol. 2, No. 2. February, 1924.

1. Ecology of the Plankton Algae in the Palisades Interstate Park,
Including the Relation of Control Methods to Fish Culture.....
Dr. Gilbert M. Smith.

ROOSEVELT WILD LIFE BULLETIN, Vol. 2, No. 3. March, 1924.

1. The Status of Fish Culture in Our Inland Public Waters, and the Role
of Investigation in the Maintenance of Fish Resources.....
Dr. William C. Kendall.
2. Current Station Notes.....The Director and Editor.

ROOSEVELT WILD LIFE BULLETIN, Vol. 2, No. 4. February, 1925.

1. The Relation of Wild Life to the Public in National and State
Parks.....Dr. Charles C. Adams.
2. The Big Game Animals of Yellowstone National Park..Edmund Heller.
3. The Food of Trout in Yellowstone National Park.....
Dr. Richard A. Muttkowski.
4. Current Station Notes.....The Director and Editor.

THE

Roose

V

Rooseve



With the compliments of

THE ROOSEVELT WILD LIFE
FOREST EXPERIMENT STATION

Syracuse, New York



Digitized by the Internet Archive
in 2015

BULLETIN

OF

THE NEW YORK STATE COLLEGE OF FORESTRY
AT SYRACUSE UNIVERSITY

HUGH P. BAKER, *Dean*

Roosevelt Wild Life Bulletin

VOLUME 5

NUMBER 4

OF THE

Roosevelt Wild Life Forest Experiment Station



ANNOUNCEMENT

The serial publications of the Roosevelt Wild Life Forest Experiment Station consist of the following:

1. Roosevelt Wild Life Bulletin.
2. Roosevelt Wild Life Annals.

The *Bulletin* is intended to include papers of general and popular interest on the various phases of forest wild life, and the *Annals* those of a more technical nature or having a less widespread interest.

The editions of these publications are limited and do not permit of general free distribution. Exchanges are invited. The subscription price of the *Bulletin* is \$4.00 per volume of four numbers, or \$1.00 per single number. The price of the *Annals* is \$5.00 per volume of four numbers, or \$1.25 per single number. All communications concerning publications should be addressed to

THE DIRECTOR AND EDITOR,
Roosevelt Wild Life Forest Experiment Station.
Syracuse, New York.

TRUSTEES OF THE NEW YORK STATE COLLEGE OF FORESTRY

EX OFFICIO

Dr. CHARLES W. FLINT, <i>Chancellor</i>	Syracuse University
Dr. FRANK P. GRAVES, <i>Commissioner of Education</i>	Albany, N. Y.
Hon. ALEXANDER MACDONALD, <i>Conservation Comm'r</i> ...	Albany, N. Y.
Hon. HERBERT H. LEHMAN, <i>Lieutenant-Governor</i>	Albany, N. Y.

APPOINTED BY THE GOVERNOR

Hon. JOHN R. CLANCY,.....	Syracuse, N. Y.
Hon. HAROLD D. CORNWALL.....	Glenfield, N. Y.
Hon. GEORGE W. DRISCOLL.....	Syracuse, N. Y.
Hon. ALFRED E. SMITH.....	New York City
Hon. WILLIAM H. KELLEY.....	Syracuse, N. Y.
Hon. EDWARD H. O'HARA.....	Syracuse, N. Y.
Hon. CHARLES A. UPSON.....	Lockport, N. Y.
Hon. J. HENRY WALTERS.....	New York City
Hon. EDMUND H. LEWIS.....	Syracuse, N. Y.

OFFICERS OF THE BOARD

Hon. ALFRED E. SMITH.....	<i>President</i>
Hon. JOHN R. CLANCY.....	<i>Vice-President</i>

HONORARY ADVISORY COUNCIL OF THE ROOSEVELT WILD LIFE STATION

AMERICAN MEMBERS

Mrs. CORINNE ROOSEVELT ROBINSON.....	New York City
Hon. THEODORE ROOSEVELT.....	New York City
Mr. KERMIT ROOSEVELT.....	New York City
Dr. GEORGE BIRD GRINNELL.....	New York City
Hon. GIFFORD PINCHOT.....	Milford, Pa.
Mr. CHAUNCEY J. HAMLIN.....	Buffalo, N. Y.
Dr. GEORGE SHIRAS, 3rd.....	Washington, D. C.
Dr. FRANK M. CHAPMAN.....	New York City
Dean HENRY S. GRAVES.....	New Haven, Conn.

EUROPEAN MEMBER

VISCOUNT GREY.....	Fallodon, England
--------------------	-------------------

ROOSEVELT WILD LIFE STATION STAFF

HUGH P. BAKER, M.F., D.Occ.....Dean of the College

CHARLES E. JOHNSON, A.M., Ph.D.....Director of the Station
 WILFORD A. DENCE, B.S.....Ichthyologist and Ass't Director
 MIRIAM S. MOCKFORD.....Secretary

Temporary Appointments*

ROBERT T. HATT, A.M.....Field Naturalist
 MYRON T. TOWNSEND, Ph.D.....Field Naturalist
 M. W. SMITH, M.A.....Field Naturalist
 JUSTUS F. MÜLLER, Ph.D.....Field Naturalist
 DAYTON STONER, Ph.D.....Field Ornithologist
 CHARLES J. SPIKER, A.B.....Field Naturalist
 LEROY STEGEMAN, M.S.....Field Naturalist
 H. J. VAN CLEAVE, Ph.D.....Field Naturalist

* Including only those who have made field investigations and whose reports are now in preparation.

GENERAL CONTENTS

	PAGE
1. The Biology of the Voles of New York. Robert T. Hatt	513
2. The Relation of Mammals to the Harvard Forest	
Robert T. Hatt	625

ILLUSTRATIONS

PLATES

Plate. 3. THE VOLES OF NEW YORK.

- 1, Meadow mouse, *Microtus p. pennsylvanicus*; 2,
Red-backed mouse, *Clethrionomys g. gapperi*; 3,
Pine mouse, *Pitymys pinetorum scalopsoides*;
4, Lemming vole, *Synaptomys c. cooperi*. . . Facing 513

FIGURES

(All photographs by the author unless otherwise stated)

Fig. 161. Poses of the meadow mouse (<i>Microtus pennsylvanicus</i>). Photographs by Richard Archbold, H. B. Sherman and Robert Hatt.	517
Fig. 162. Hummock growth at the border of a hardwood swamp. Bedford, N. Y. <i>Microtus</i> were uncommon here.	518
Fig. 163. Hummock growth in a swamp at Bedford, New York. <i>Microtus</i> and <i>Zapus</i> were common here.	518
Fig. 164. The effect of burning in a typical meadow mouse habitat of Westchester County, N. Y. The annual fires often burn more thoroughly than shown here. April 8, 1928.	525
Fig. 165. Hoar frost in the swamp in winter. The inhospitable winter conditions in these areas are a major factor in keeping down the mouse populations, and in causing them to move to the uplands in the winter. Bedford, N. Y. December, 1928.	525
Fig. 166. Rank herbaceous growth at the swamp border. Here <i>Microtus</i> is very abundant. Bedford, N. Y.	526
Fig. 167. Wet upland field inhabited by <i>Microtus</i> . Ann Arbor, Michigan.	526
Fig. 168. Dry pastured field, Bedford, N. Y. Grazing and aridity are responsible for keeping meadow mice from such a field as this.	537
Fig. 169. Fields, Bedford, N. Y. The fields in the extreme distance that are unpastured support a meadow mouse population. Those in the foreground and to the right are uninhabited.	537
Fig. 170. Mouse runways in a small dry field exposed by burning. The grass here had not been cut in three years, and the mice did great damage in the nearby garden. Bedford, N. Y.	538
Fig. 171. Excavated earth marking the course of burrows used by meadow mice in a Bedford, N. Y., marsh.	538
Fig. 172. Three nests of meadow mice, unusually close together. Bedford, N. Y. April 27, 1929.	547
Fig. 173. A nest of <i>Microtus</i> , lifted from its site. Bedford, N. Y. April 27, 1929.	547
Fig. 174. A typical nest of <i>Microtus</i> , Bedford, N. Y. April 27, 1929.	548
Fig. 175. <i>Microtus</i> nest in the center of a hummock. Bedford, N. Y.	548
Fig. 176. Sloop Island, Lake Champlain, N. Y., occupied by seven <i>Microtus</i> . August 23, 1926.	557
Fig. 177. Small apple tree girdled by mice that flourished in the uncut grass nearby. Bedford, N. Y.	557
Fig. 178. Hummock, the site of a meadow mouse nest containing young. This hummock is completely surrounded by water. Bedford, N. Y. April 27, 1929.	558

Fig. 179. Meadow mice, one to two days old, in their opened nest. Bedford, N. Y.....	558
Fig. 180. Quadrats A and B, shortly after completion. Bedford, N. Y. June 21, 1927.....	567
Fig. 181. Quadrat B in foreground, Quadrat A in rear. August 7, 1927...	567
Fig. 182. Like the work of a diminutive beaver; young cork elms felled by meadow mice in Quadrat B. August 7, 1927.....	568
Fig. 183. The result of crowding. Small trees cut down in Quadrat B. August 7, 1927.....	568
Fig. 184. Detail of Quadrat fence to show the method of joining the sheet iron to the screening.....	575
Fig. 185. Red maple trees in Quadrat B, cut down and barked by meadow mice. August 7, 1927.....	575
Fig. 186. The result of a small scale plague. Quadrat B. April 8, 1928..	576
Fig. 187. The summer after the mouse damage. Quadrat B. Contrast the area of Quadrat A in the background. June 10, 1928.....	576
Fig. 188. Norway pine plantation on the border of Kensico Reservoir, New York City water system, showing conditions conducive to mouse injury. Norway pine fortunately is comparatively immune to this sort of damage.....	607
Fig. 189. Dry upland field, Bedford, N. Y. The meadow mice move into this situation in winter and in the more favorable summers...	607
Fig. 190. The method of bridge-grafting a mouse girdled tree. Redrawn from Ballou.....	608
Fig. 191. Pure stand of white pine, age 55 years. South of Harvard Pond. The trees in the foreground have been artificially trimmed of their lower branches. August 10, 1925.....	633
Fig. 192. White pine, hemlock, and transition hardwood east of Harvard Pond. August 10, 1925.....	633
Fig. 193. Red spruce swamp, north of Tom Swamp. September 3, 1925..	634
Fig. 194. Red squirrel midden of red spruce cones, typical of those common in the swamp shown in figure 193. September 3, 1925...	634
Fig. 195. Twigs of larch clipped by a red squirrel in a plantation in the Harvard Forest. Photograph by A. C. Cline.....	641
Fig. 196. Laterals of twenty-foot European larch whose twigs have been clipped by red squirrels in a previous winter. June 27, 1925...	641
Fig. 197. The central part of a larch stem showing stumps of twigs winter-cut by red squirrels. August 25, 1925.....	642
Fig. 198. A twenty-five-foot larch defoliated by red squirrels' winter-clipping of laterals. June 27, 1925.....	642
Fig. 199. Another larch showing typical red squirrel injury. August 25, 1925	642
Fig. 200. Scotch pine plantation on the Harvard Forest showing the bushy growth resulting from repeated red squirrel injury. Photograph by A. C. Cline.....	649
Fig. 201. Scotch pine plantation near Speculator, New York, showing no mammal damage. Contrast the straight regular growth here seen with the deformed trees figured above. June 24, 1926...	649
Fig. 202. A "broom" forming the leader of a Scotch pine. This competitive growth of many laterals is due to the destruction of winter buds by red squirrels. September 10, 1925.....	650
Fig. 203. The same "broom" shown in figure 202, with the foliage removed. September 12, 1925.....	650
Fig. 204. The crown of a six-foot Norway spruce with the terminal and lateral twigs cut by red squirrels the winter previous. June 27, 1925	653
Fig. 205. The crown of a five-foot white spruce of Valcour Island, Lake Champlain, New York, with the leader cut by red squirrels. August 26, 1926.....	653
Fig. 206. Branch tips of Norway spruce with winter buds hollowed out by red squirrels. January, 1926.....	654

	PAGE
Fig. 207. The crown of a nine-foot Norway spruce showing twinning of leaders apparently caused by red squirrel clipping a leader in a previous winter. June 27, 1925.....	654
Fig. 208. Larch girdled by porcupine on the Harvard Forest. Photograph by A. C. Cline.....	661
Fig. 209. Two mature hemlocks with all small twigs clipped by feeding porcupine. Photograph by A. C. Cline.....	661
Fig. 210. The base of a Scotch pine completely girdled by mice. North Ashburnham, Massachusetts. July 18, 1925.....	662
Fig. 211. A Scotch pine girdled by mice which has sent up a new shoot from the base to replace the dead stem. September 10, 1925..	662
Fig. 212. A small group of Scotch pines killed by mice. North Ashburnham, Massachusetts. July 18, 1925.....	667
Fig. 213. Pure growth white pine. Harvard Forest. August 10, 1925....	667

1

2

3

4

SAWYER

PLATE 3. THE VOLES OF NEW YORK

1. Meadow mouse, *Microtus p. pennsylvanicus*
2. Red-backed mouse, *Clethrionomys g. gapperi*
3. Pine mouse, *Pitymys pinetorum scalopsoides*
4. Lemming vole, *Synaptomys c. cooperi*

D. C. Mac Lulich

THE BIOLOGY OF THE VOLES OF NEW YORK

BY ROBERT T. HATT*

*Field Naturalist, Roosevelt Wild Life Forest Experiment Station,
Syracuse, New York*

CONTENTS

	PAGE
Introduction	514
Description of the New York Species of Voles.....	516
Aquatic Adaptation in <i>Microtus</i>	520
Habitats	521
Runways and Burrows.....	527
Nests	530
Stores	531
Time of Activity.....	534
Social Traits and Disposition.....	534
Intercommunication	536
Destructive Agencies of Voles.....	539
Food	563
Quadrat Studies	572
Effect of Vole Feeding on Farming.....	578
Good Services of Voles.....	584
Breeding	586
Populations	593
Mouse Plagues	597
Control of Microtine Populations.....	610
Protection of Fruit Trees from Mice, and the Saving of Injured Trees	615
In Conclusion	617
List of References.....	619

*Assistant Curator of Mammals, The American Museum of Natural History, New York City.

INTRODUCTION

The voles are a key-industry in Nature. They convert the vegetation into flesh on which a large number of other species are dependent. Numerous snakes, birds of prey and carnivorous mammals subsist principally on these microtines, and many other animals feed on them, in some form or other, as occasion offers. Their numbers and wide distribution make their importance to all this other life great; and their own choice of food gives them often particular importance to man. No other group of mammals is, perhaps, generally speaking, of greater agricultural interest, for wherever found they are generally looked upon as a menace, real or fancied, to crops of certain kinds and in times of excessive abundance they may inflict damage on a considerable scale.

More than other groups of mice, the microtines are subject to marked fluctuations in their populations. In times of greatest abundance we have a "mouse year" or a "mouse plague." "These violent outbreaks," says Huxley (in Elton, '27, p. xvi), "are but special cases of a regular phenomenon of periodicity in numbers which is perfectly normal for many of the smaller mammals. The animals, favored by climatic conditions, embark on reproduction above the mean, outrun the constable of their enemies, become extremely abundant, are attacked by an epidemic and suddenly become reduced again to numbers far below the mean." In the classical cycles of abundance among the lemmings of Norway, and in other more sporadic outbreaks, a wave of migration takes place from the area of over-population. It is then that conspicuous damage is done by the hoards, and public interest is aroused. But at all times the microtines lay a certain tax on agriculture, and their economic import is in the mean greater than in occasional bad years. Whether or not the voles render a service equal to the amount of their toll, we shall have to consider from the evidence.

The phases of economic importance of the voles, other than the outstanding agricultural one, are several. There is apparent dissemination of disease by their agency in some quarters. The Japanese *Microtus montebelloi* is believed to be one of the carriers of infectious jaundice and Japanese river fever. Meadow mice in Europe have spread erysipelas of swine, aphthous fever and other diseases. The role of fossorial microtines in the production of a fertile soil in some tracts that would otherwise be barren, can be appreciated.

Like the earthworms, moles and pocket gophers, they are continually at work in the development of cultivatable land. As the mechanism which turns weeds and waste vegetation into food for our fur bearers and other flesh eaters, the voles as a group have no equal.

The microtines constitute a large subfamily of the rodent family *Cricetidae*. They include such forms as the voles, the lemmings and the muskrat. Their numbers are distributed throughout the Holarctic Region from the limits of terrestrial mammalian life in the far North to the Alpine meadows of Guatemala mountains and, in the Oriental region, to those of Yunnan and Burma. They are, in recent time, absent in Northern Africa. Vertically they range from sea-level to the limits of mammalian life, at about 20,000 feet in the Himalayas.

The greater number of the species are extensive burrowers and many are semi-aquatic. In appearance they are robust, short-eared, blunt-nosed mice; and their legs appear short because of their loose belly skin and long fur.

There is no vernacular name which applies well to the entire group. Outside the United States, English speaking people commonly call them "voles". This term is now generally in use in our scientific publications, but it has not come into vogue with the larger number of people who know them. They are usually called "meadow mice" or "field mice", neither of which is a perfect term. "Field mouse" is used for the long-tailed mice of several genera, as well as for the voles. "Meadow mouse" is open to objection in that many of the voles live in forests and other habitats, aside from meadows. The term meadow mouse does apply well to our common eastern form (*Microtus pennsylvanicus*) and will be used to designate this species and its nearest allies. There are, however, various local names in use for the meadow mouse such as meadow-mole, bear mouse, buck-tailed mouse and black mouse.

In North America, at least, the voles of the genus *Microtus* are of greater agricultural and silvicultural importance than are all the related genera combined, and it is with the members of this genus, therefore, that we are principally concerned. Three other voles occurring within New York state have varying degrees of economic interest. These are the red-backed mouse (*Clethrionomys gapperi*), the pine mouse (*Pitymys pinctorum scalopsoides*) and the lemming vole (*Synaptomys cooperi*). The last named is represented in the southern corner of the State by a southern subspecies (*S. cooperi stonci*).

DESCRIPTION OF THE NEW YORK SPECIES OF
VOLES

Meadow Mouse (*Microtus pennsylvanicus pennsylvanicus*). The meadow mouse (Plate 3 and Figure 161) is a medium sized thick bodied vole with rather long loose pelage, legs of medium length and a tail about twice the length of the hind foot. The tail is scaly and thinly covered with short hair. The ears are short, furred along their borders, and practically hidden in the surrounding fur of the head.

The pelage aside from being long and loose, is rough in appearance. The upper parts in summer are a chestnut brown, varying with the individual to yellowish chestnut, sprinkled with black along the back. The underparts are gray with a dusky tinge, or washed with cinnamon. The feet are brownish. The tail above is dusky, below slightly paler. The winter pelage is grayer than the summer, though the difference is not marked. The sexes are colored alike. Young individuals are darker than adults, appearing blackish.

"Their fur," according to Bailey ('24, pp. 527-528), "is fairly waterproof, and when wet quickly dries as it is carefully combed and cleaned. After working in the earth the mice clean their nails and comb their fur, which they usually keep in perfect condition. Without plenty of water or dry earth, the fur becomes oily and rough, but either water or sand removes the excess oil and leaves it light and fluffy."

On the sole of the hind foot are six tubercles. The thumb is vestigial. The upper incisors are simple and ungrooved.

The average measurements of a series of eighteen adult *Microtus pennsylvanicus* from Bedford, New York, taken between June 18 and August 26, 1927, were as follows. The adults were separated from immature specimens by criteria based on the condition of the reproductive organs, measurements and general appearance. There was some overlapping in the series, particularly in regard to weight: Total length, 159.4 (143-183) mm; tail length, 41.8 (35-50) mm; length hind foot, 21.3 (20-22) mm; height of ear from crown, 10.6 (9-14) mm. Total weights, 42.9 (30.7-62.7) grams. After eliminating the five pregnant females from the group, an average weight of 39.9 (30.7-54.5) grams is obtained. The heaviest included in the average contained an enlarged, though empty uterus.

Pine Mouse (*Pitymys pinetorum scalopsoides*). The pine mouse (Plate 3) is smaller than the eastern meadow mouse and has short



Fig. 161. Poses of the meadow mouse (*Microtus pennsylvanicus*). Photographs by Richard Archbold, H. B. Sherman and Robert Hatt.



Fig. 162. Hummock growth at the border of a hardwood swamp. Bedford, N. Y. *Microtus* were uncommon here.



Fig. 163. Hummock growth in a swamp at Bedford, New York. *Microtus* and *Zapus* were common here.

smooth glossy fur which gives it a mole-like aspect. The tail is short and well furred. It scarcely exceeds the length of the hind foot. The ears are very small and hidden in the fur.

The pelage above is a dull brownish chestnut, sprinkled sparingly with dusky; sides paler. The under parts are washed with dull buff. Seasonal, sexual, and age variation is slight.

There are but five tubercles on the sole of the hind foot.

The average measurements of three adults from Lake Grove, Long Island, as given by Bailey ('00, p. 64), are: total length, 125 mm; tail vertebrae, 20 mm; hind foot, 16.3 mm.

Red-backed Mouse (*Clethrionomys gapperi gapperi*). The red-backed mouse (Plate 3) is a small to medium sized mouse, with furred ears that reach above the pelage, a tail longer than the hind foot, and fairly long fur.

The pelage is marked with a bright chestnut dorsal band extending from the crown to the base of the tail. The sides are buffy ochraceous. The underside is a pale buff. The feet are clear gray; the tail bicolor, brownish above, black tipped grayish buff below. The summer pelage is slightly darker. Sexes are colored alike. The immature pelage is more subdued in coloration.

The average measurements of ten adults from Elizabethtown, N. Y. (Bailey, '97, p. 123), were: total length, 141 mm; tail vertebrae, 39 mm; hind foot, 18.3 mm.

Lemming Vole (*Synaptomys cooperi cooperi*). The lemming vole (Plate 3) is externally much like the meadow mouse, but is smaller and has a much shorter tail. It is further easily differentiated by a conspicuous longitudinal groove near the lateral edge of the upper incisors.

The upper parts are a mixed gray, yellowish brown and black, giving a grizzled appearance similar to cinnamon-brown. The under parts are a soiled whitish wash over a slate-colored underfur. The bicolored tail is brownish above and whitish below. The sexes are alike. Immature individuals are darker and more slatey than the adults.

There are six plantar tubercles. The nail of the greatly reduced thumb is flat and strap-shaped.

Measurements of the five largest individuals from a Quebec series were (Howell, '27, p. 13): total length, 118 mm; tail vertebrae, 16.5 mm; hind foot, 18 mm.

Specimens from the southern corner of New York are referable to the subspecies *S. cooperi stonci*, but in the field are indistinguishable from the northern race.

AQUATIC ADAPTATION IN MICROTUS

Floods commonly occur in those habitats in which *Microtus* reaches its greatest abundance, and to conditions consequent to such flooding *Microtus* is adapted. These voles are very capable swimmers, taking to water fearlessly, swimming rapidly and emerging without being unduly wetted. Their fur is dense, like that found in many natatorial mammals, such, e.g., as their first cousin, the muskrat. In swampy areas (Figs. 163, 165, 175, 178) their nests are built in the crowns of the hummocks of grass commonly known as "nigger heads". In these nests the young are born, and in such areas underground tunnels are rare. The tops of the "nigger heads" in all ordinary floods remain above water and form many small islands. At such periods the small young must of necessity remain in their nests, and the adults must spend much of their time in swimming when out foraging. Such an ordinary period of high water occurred in a certain five-acre swamp in Bedford township, New York, for the fourteen days from August 26 to September 8, 1927. At the edge of the swamp, where the voles were in their greatest concentration, all runways were covered with water from one to five inches deep, while in the greatest area of "nigger heads" water stood eight to twelve inches deep. At the border zone of runways and burrows, where nests were closer to the ground, the mice were forced out from their preferred home, but in the hummock region they may have held their own. This flooding, I believe, does not greatly decrease the numbers of the mice, though it may expose them more to their enemies. Of course floods suddenly covering large areas with deep water all but wipe out the various species of the mice, though I presume *Microtus* fares as well as or better than most of the other small forms.

In flooding, the young are not of necessity doomed. Water usually rises slowly enough to allow the parents to remove them to safer quarters. The parents are well able to move their litter by swimming; and the helpless young, it appears, are able to stand remarkably long submersion, as the following instance indicates. A new-born *Microtus pennsylvanicus*, secured September 11, at Bedford, New York, was immersed in cold water and brushed free of all air bubbles. It was held thus for 30 minutes. At this time, believing it dead and ready for preservation, I removed it. Immediately it breathed convulsively, and was put back in the water before a second inhalation could be made. Fifteen minutes more it was kept under

water. Then, upon being touched, it moved, showing that it still retained life. At the end of another fifteen minutes under water, it failed entirely to respond, whereupon it was removed and preserved as a specimen.

With regard to the aquatic habits of *Microtus*, Audubon and Bachman ('54, Vol. 1, p. 344) offer the following observation: "Wilson's meadow mouse swims and dives well. During a freshet which covered some neighbouring meadows, we observed several of them on floating bunches of grass, sticks, and marsh weeds, sitting in an upright posture as if enjoying the sunshine, and we saw them leaving these temporary resting places and swimming to the neighbouring grounds with great facility; a stick thrown at them on such occasions will cause them to dive like a muskrat."

HABITATS

Habitats of the Meadow Mouse. Meadow mice are most at home in meadows or in rank growth bordering marshes, lakes or water courses. They will, however, adapt themselves to very diverse conditions if food and shelter are available. They will, as already suggested, live in flooded marshes, swimming from one tussock to another, and will cross streams. Under crowded conditions they will move out into dry fields, orchards, and gardens, but seldom become established in such situations for a whole season. Though *Microtus* can probably satisfy all its physical requirements in a forest, it is almost unknown in such situations. A striking exception occurs on a small island in Lake Michigan, where Dice ('25b, p. 3) took it in numbers in a forest in which Norway pine was dominant in some places, and hard maple in others. It was as common as in the more normal marsh habitat. In some sections of the West these mice have become particularly troublesome because of their activities in burrowing into the banks of irrigation ditches.

At Bedford, N. Y., in times of average population, which was apparently well illustrated by the summer of 1927, *Microtus* is practically limited to the swamps and marshes and their unwooded borders (Figs. 163 to 166). Pioneers constantly push out into other habitats and in years of heavy population or unusual wetness they may become well established. Such local spacing of *Microtus* may be suggested by the results of a small amount of trapping carried on in the summer of 1927, in these habitats, in which the presence or former presence of *Microtus* was evidenced chiefly by the nests typical of this animal:

STATION 1. Proximity of an intermittent (dry when trapped) and wood-bordered watercourse passing down a hillside field into a red maple swamp.

The common trees of the habitat were sweet birch (*Betula lenta*); shagbark hickory (*Carya ovata*); rum cherry (*Prunus scrotina*); pin cherry (*Prunus pennsylvanica*); cork elm (*Ulmus racemosa*); red maple (*Acer rubrum*). Other trees occurring were red cedar (*Juniperus virginiana*); chestnut (*Castanea dentata*) and butternut (*Juglans cinerea*). Ferns of several species were common, among these the maiden hair and the sensitive fern. Staghorn sumach (*Rhus typhina*) and hackberry (*Celtis occidentalis*) were among the more common shrubs.

Trap nights, 96; June 15 to 20: *Microtus*, 1; *Synaptomys*, 1; *Peromyscus*, 7.

STATION 2. Relatively dry meadow, grown to grasses, blackberry, sensitive fern, etc. This is the area surrounding the quadrats elsewhere described (Fig. 180).

Trap nights, 102; June 15 to 20: *Microtus*, 0; *Peromyscus*, 2. Several old *Microtus* nests were found.

STATION 3. This station was an uneven, dry, grassy field, little encroached upon by cedars or other large plants. In its lower section the grass of the year before lay deep, while on the gentle slope to this lower section the soil was nearly barren. There was little new growth at the time of trapping (Fig. 189).

The common plants, other than grasses, were rattlesnake weed (*Hieracium venosum*); loosestrife (*Lysimachia quadrifolia*); goldenrod (*Solidago* spp.); white flowering and yellow flowering brambles (*Rubus* spp.); and red cedar (*Juniperus virginiana*). There were, too, a few bayberry (*Myrica carolinensis*) and huckleberry (*Vaccinium* sp.) shrubs.

In the area of long dry grass — forming a heavy blanket as much as eighteen inches deep over the ground — *Microtus* runways and old nests were common, apparently of the previous year, during which there was a luxuriant growth of vegetation.

Trap nights, 213; June 16 to 20: *Microtus*, 2. Trap nights, 90; August 19 to 24: *Microtus*, 2.

STATION 4. Marsh at the intersection of the Bedford-Cross River and the Poundridge roads, crossed and drained by the Saw Mill River (Figs. 163, 165, 166, 175, 178).

In this habitat the following plants were conspicuous: Alder and willow (along the stream), swamp grass, sedges (*Carex scirpoides*, *C. stipata*, *C. setacea*, *C. hystericina*); rush (*Juncus balticus*, var.

littoralis) ; blue flag (*Iris versicolor*) ; skunk cabbage (*Symplocarpus foetidus*) ; tall buttercup (*Ranunculus acris*) ; arrowhead (*Sagittaria latifolia*) ; swamp orchis (*Habenaria flava*) ; bedstraw (*Galium palustre*) ; small forget-me-not (*Myosotis laxa*) ; bur-reed (*Sparganium diversifolium*) ; chain fern (*Woodwardia virginica*) ; sensitive fern (*Onoclea sensibilis*).

In this habitat, the following vertebrates were common: Brook trout, leopard frog, green frog, bullfrog, spring peeper, spotted turtle, painted turtle, mud turtle, snapping turtle, black snake, little green heron, red-winged blackbird, Maryland yellow-throat, muskrat; and, on one side of the stream, cattle and mules.

Trap nights, 265; June 20 to 26: *Microtus*, 14; *Zapus*, 4. Trap nights, 75; August 24 to 28: *Microtus*, 13; *Zapus*, 2.

The spacing of nests in three instances were respectively as follows:

A. Bedford, New York. Marsh and marsh border at intersection of Bedford-Cross River with the Poundridge roads. Area to west of stream part of Station 4, as defined above (Figs. 172, 174, 175, 178). Census taken April 27, 1929, about two months after the area had been thoroughly burned. The section considered had an area of 15,000 square feet (.34 acre). On it were 72 nests (1:208 square feet), 18 (1:833 square feet) of which were apparently in use.

B. Locality as above, except that it was situated on the opposite bank of the stream where there was heavy grazing by cattle and mules. Census taken June 28, 1927. The section considered had an area of 6,000 square feet. On it were 6 nests (1:1000 square feet), three of which were in use (1:2000 square feet).

C. Sloop Island, Lake Champlain, New York (Fig. 176). The entire vegetated area of this small island (see Hatt, '28). Census taken early in September, 1926. The area considered was 1,100 square feet. On it was one nest (1:1100 square feet), two adult and five young *Microtus* of one litter.

The only attempt to make an accurate qualitative analysis of the environmental needs of meadow mice is that of Dice ('22, pp. 29-47) for the prairie species, *M. ochrogaster*. He found that if there was green grass for food, no water was necessary, while dry grass could be utilized if water was available to the extent of 6 cc. daily, with a temperature around 21° C, and an air humidity of 50 per cent. Areas that undergo an annual period of drought are not inhabited by this species, and the occasional lack of water or succulent vegetation appears to be the factor limiting its westward spread.

Temperatures above 36° C (96.8°F) were critical for this species, and it may well be that its southern limits are controlled by this temperature line. Eastward the limitation is presumed to be that of

habitat for there are no known climatic factors there which would appear unfavorable.

Habitats of the Pine Mouse. The pine mice live almost entirely in burrows which they construct in the light dry and loamy soils, either within, or outside of, wooded areas. They usually avoid rocky and swampy lands, though on occasions they may temporarily, at least, occupy such localities.

In Bedford township, New York, the only places where I have found these mice have been in small vegetable and flower gardens in loamy soil, partly shaded by trees. In both instances the animals followed the rows of vegetables, and did considerable damage by feeding on the roots of the various plants.

Habitats of the Red-backed Mouse. The red-backed mouse is the vole of the forest. It has a chestnut hue which blends with its chosen background. *Clethrionomys* seems to prefer damp places where it can have free access to water.

In the southern part of its range it is restricted in its distribution to damp evergreen forests and sphagnum bogs.

In Leelanau County, Michigan, I found (Hatt, '23, p. 396) the red-backed mice most abundant near a stream in an arbor vitae swamp. Most specimens were taken under logs that were elevated above the ground. No runways were seen here.

In Petersham, Massachusetts, I found red-backed mice common in a red spruce swamp, in pine forest (Figs. 191 and 193) and in mixed forest. In a wet, fern grown depression in an otherwise dry pine forest, I took three red-backed mice on successive nights, in a single trap. Several traps set on drier ground within a two hundred-foot radius failed to catch a single mouse of this species.

Habitats of the Lemming Vole. Of all our microtines, *Synaptomys* is the most irregular in its distribution. It inhabits a wide variety of habitats, but has only been found abundant on a few occasions in a few places. In the East, according to Stone and Cram ('03, p. 107), the cold sphagnum bogs seem to be the favorite haunts of this species. Rhoads ('03, p. 107) says of its distribution in Pennsylvania and New Jersey that he has never taken true *cooperi* in woodland, but generally in "swampy mountain clearings near woods, among dense grass and weeds". *S. cooperi stonci*, on the other hand, he found to be confined to sphagnum bogs. The one specimen which I have taken in New York State was from the habitat described on page 522 as station I. Burt ('28, p. 213)



Fig. 164. The effect of burning in a typical meadow mouse habitat of Westchester County, N. Y. The annual fires often burn more thoroughly than shown here. April 8, 1928.



Fig. 165. Hoar frost in the swamp in winter. The inhospitable winter conditions in these areas are a major factor in keeping down the mouse populations, and in causing them to move to the uplands in the winter. Bedford, N. Y. December, 1928.



Fig. 166. Rank herbaceous growth at the swamp border. Here *Microtus* is very abundant. Bedford, N. Y.



Fig. 167. Wet upland field inhabited by *Microtus*. Ann Arbor, Michigan.

gives the following account of its distribution in Kansas:—"Most of the *Synaptomys* secured by the several collectors of the University of Kansas Museum have been taken in or near blue grass associations where the grass had grown up from year to year and formed a thick mat that provided ideal feeding grounds as well as shelter. Seven miles southwest of Lawrence a number of *Synaptomys* were caught at the edge of a blue grass patch near a creek where there was an undergrowth of grass of the genus *Setaria* among some dry weeds. Others were caught in a patch of blue grass on a north-facing slope near the top of a high hill one and one-half miles west of Lawrence. In wet weather this patch of grassland is decidedly 'seepy' and a clump of willow trees grows at one edge. Near this place traps were set in dry grass, in weeds, and along fence rows, but only one specimen was caught away from the blue grass. This was an adult male caught February 26, 1926, in a runway through some dry weeds about one-fourth mile from any blue grass. On a previous night a specimen of *Microtus ochrogaster* was caught in the same trap and on the following night a specimen of *Cryptotis parva*. In several instances *Synaptomys* and *Microtus* were caught in the same runs."

In Indiana (Quick and Butler, '85, p. 114), "This mouse is found on hillsides in high, dry, blue grass pastures, where flat stones are irregularly scattered over the surface; it especially prefers what are known as 'woods pastures', containing little or no undergrowth."

In Michigan, I have taken *Synaptomys* at the border of a cedar swamp, in a rank herbaceous growth along a small stream, and in brushy fence rows between cultivated fields. Dice ('25a, p. 24), in Charlevoix County, Michigan, took the species in the following habitats: fir and spruce second growth forest, arbor vitae swamp, swamp brush, and hardwood second growth forest. In Northern Michigan, Dice and Sherman ('22, p. 30) secured specimens in tall sedge, black spruce tamarack bog, and hardwood forests.

RUNWAYS AND BURROWS

The Runways and Burrows of the Meadow Mouse. The universal indication of the presence of a *Microtus* colony is the labyrinthine network of runways which covers the surface of the ground. These pathways, which are from one to two inches in diameter, are constructed by the mice themselves. At first the grass is merely parted and pushed aside, or trampled down somewhat, but eventually the stems are cut away so that the naked earth is exposed. With

constant use, and the carry-off of rains, these pathways may even sink below the level of the ground. The grass arches over these runways, if it has not been too closely cropped or burned, and affords a canopy under which the mice can run for long distances, more or less completely shielded from enemies above.

When there is serious crowding in a *Microtus* colony, the grasses may be so closely cropped for food by the mice that the runways are merely denuded grooves in a short stubble covering the area (similar to the condition seen in Fig. 170). Such was the condition on Sloop Island, Lake Champlain, in early September, 1926 (Hatt, '28, p. 92).

The system of surface runways is doubtless extended primarily during foraging activities. They are kept free from obstructions as if to permit unhindered passage in emergency.

Underground burrows are developed extensively in connection with the surface runways, and these burrows are inclined to be as intricate as the paths above them. The burrows vary in their depths below the surface, but the roofs are never arched up in the fashion of the tunnels of the garden mole. Burrows lead to buried stores, to underground nests and occasionally to open water. They are extensively used for escape when the overhead covering is poor.

Microtine Burrows in a Bedford Marsh. In the meadow (Station 4) at Bedford, New York, in which I found *Microtus* more abundant than elsewhere in the town, there is a great labyrinth of burrows. These average six inches below the surface, and in periods of average water are but an inch above the water table. At times large sections of the burrows are flooded. The diameter of these burrows averages 2 to 2½ inches. At intervals of about ten feet along the burrows are great plugs of rich black earth, pushing up above the ground and forming mounds averaging eight inches across and four inches high, the accumulation of earth disposed of (Fig. 171) in burrowing. I have frequently removed these plugs and set traps at the holes, but each time the trap was covered with earth by the digging animals. Traps set across the underground runways were similarly clogged, while mole traps were never sprung. These runways sometimes connect with concealed entrances to above-ground nests, and I have found one small chamber lined with wet grass, pocketing off such a burrow. Though I knew that *Microtus* used these runways, I was not convinced that they were not primarily the work of star-nosed moles. I have never taken the latter species in this habitat, but the burrows were suggestive of that animal.

Burrows of the Pine Mouse. The pine mouse is the most fossorial of our microtines. It leaves its burrow infrequently, and feeds there almost exclusively. Even the feeding posture has been adapted to this mode of life, for, unlike its other relative, the pine mouse does not sit up to eat, but stays down on all fours. The hair is short, fine, and even textured, reminding one much of that of the shrews. The ears and tail are short, as in most other burrowers, the eyes small and the fore feet slightly enlarged.

Rhoads writes of its tunnels in New Jersey ('03, p. 103): "Being less powerful than the mole, it confines its tunnels to looser soils, preferring sandy, fallow ground for its foraging, and is especially fond of cultivated fields along the edge of the woodland. . . . In some sweet potato fields scarce a square foot of the whole field adjoining the woods was left unvisited. . . . It does not hesitate to use the burrows of the mole; in fact, moles, shrews, deer mice and pine voles make full use of each other's highways, in a most democratic fashion." Kennicott ('57, pp. 102-103) states that in attempting to escape, these mice "ran *under* instead of *over* the leaves, even where there were no paths. . . . When placed on the snow it attempts to burrow into it instead of running on top."

The burrows have numerous openings to the surface, from which the mice forage to some extent. The diameter of the burrows is usually about three quarters of an inch. The roof is sometimes arched up like that of a mole's burrow, but usually the burrow lies too deep for such arching to occur.

Runways and Burrows of the Red-backed Mouse. In most locations the red-backed mice do not have well marked surface runways like those of the meadow mice. The nature of the forest floor perhaps rarely makes it necessary. They rather roam at will within their favorite haunts. On the other hand, they may build extensive burrows. Rhoads ('03, p. 94) writes that he has "found their burrows forming such a perfect network through the moss that scarce a foot of the sphagnum could be found without one or more of them, rarely coming to the surface, but mostly running at or below the level of the hidden springs which feed the swamp."

In the cedar swamps, where I have found them most abundant, and in other drier woodlands their tunnels seemed to be confined to short branching passages leading to small chambers under logs and stumps.

Runways and burrows of the Lemming Vole. It appears from all accounts that *Synaptomys* travels largely in the runways and burrows of his more abundant cousin, the meadow mouse. But doubtless runways are often shared with any other small mammals, also, of the same habitat.

NESTS

Nests of the Meadow Mouse. The nests of *Microtus* are usually located in two different types of sites, above ground (Figs. 172, 174 and 175) and in pockets along their tunnel systems underground. The above ground nests are by preference well concealed in a heavy mat of grass or in the center of a luxuriant tussock (Figs. 175 and 178). They are commonly constructed of dry grasses, sedges, and pieces of weeds that grow near at hand. The interior is usually lined with finer material than that of the outer bulk of the nest. Sometimes it is the silky parachutes of milkweed seeds or the down from a cat-tail spike. More often it is but more finely shredded material of the same kind as that of the exterior.

Nests found above ground in the town of Bedford, New York, have been constructed almost entirely of grass; but occasionally a little green moss is used as well. They are nearly perfectly globular (Fig. 173), and their cavity is usually in the center of the ball. There may be one or two entrances to the nest, either one or both leading to a surface runway or an underground burrow.

"The nests are kept clean while in use," writes Bailey ('24, p. 528). "and are abandoned when they get old and stale. New nests with soft linings are usually prepared a few days in advance for each litter of young, so that new nests or fresh linings are generally provided about every 20 days."

Underground nests are smaller than those hidden in the grass, but are composed of similar material. They appear to be more frequently occupied in winter than in summer.

Nests of the Pine Mouse. It is not my fortune to have had any personal acquaintance with the nests of pine mice. Kennicott ('57, p. 103) wrote of them: "I have always found the nest of this arvicola under logs or stumps, whether that of the female, with her young, in summer, or pairs in their winter-quarters in November. Those observed in fields always burrow under stumps or fences, instead of the open ground. The nest in the woods is composed of leaves cut up into small fragments with fine grass. It is not placed in the underground burrow, but on the surface, being well protected by the log or roots above."

Rhoads ('03, p. 104) has a somewhat different account, as he writes: "On April 19, 1901, my man plowed over the nest of this species set at a depth of eight inches under the soil in an open field, and captured the parents with 5 young all in the same burrow." According to Quick and Butler's ('85, p. 116) account, "As a rule the pine mice winter in a last summer's nest, which is a round ball of blue grass blades, from four to six inches in diameter; the interior is composed of fine grass which is nicely bound together with longer blades. The nest is generally placed beneath a pile of leaves or an old stump. In winter collecting, single specimens are generally observed occupying these old nests."

Nests of the Red-backed Mouse. *Clethrionomys* constructs bulky nests of dry vegetable matter, grass, herbs and moss. This nest may be located under or in stumps or logs, in chambers off their burrows, or in available spaces in old stone fences.

Nests of the Lemming Vole. Of the nests of *Synaptomys*, Quick and Butler ('85, p. 114) write: "The nest of this species is always under cover, generally in a hollow log or stump, and is composed of fine grass. It is not so securely built as the nests of some of the other species of this family." Hahn ('09, p. 523) states that Quick and Butler are in error as to the statement that the nest always is under cover, as he has found a nest quite exposed, though inconspicuous. To this Burt ('28, pp. 213-214) has added the further information that "The nests, which are from six to eight inches in diameter, are made of dry grass with, sometimes, a lining of fur. In winter the nests may be found from four to six inches below the surface of the ground, while in summer the mice often build above the ground. A round cavity in which the nest is built is hollowed out in the runway. There are usually three or four exits from the nest, but it is not uncommon to find only two. A large nest built above the ground and constructed wholly of dry grass, that was found on October 30, 1925, was eight inches in diameter. The blue grass had grown up and fallen over, so that the nest was entirely concealed."

STORES

Stores of the Meadow Mouse. Many of the meadow mice in various parts of the world have taken to storing food supplies in their underground chambers. According to Bailey ('24, pp. 531-532), the storage takes place in the times of abundance and especially in autumn. He further writes: "In other parts of the country vari-

ous roots, tubers, and bulbs are stored. In captivity the mice will often secrete all surplus food under or near the nest, sometimes filling their nest boxes full of seeds, grains, and vegetables. In cold weather when the young are about to be born, the mother stores up all spare food and places it around the nest where it can be reached without her leaving the delicate, naked young, or exposing them to the cold. Approaching maternity may often be noted by this habit."

One form of the meadow mouse has earned the name "bean mouse" because of its extensive storing habits. Of these habits Bailey ('20, p. 70) writes: "In 1804 Lewis and Clark obtained from the 'Ricaras' (Arikara Indians) 'a large rich bean which they take from the mice of the prairie which discover and collect it.' Later they reported artichokes taken from the stores of mice by their Indian woman, and while Coues in a footnote credits these stores to pocket gophers, they were more probably the collections of the mice which commonly store the beans, artichokes, and other roots together in underground cavities. Other explorers give passing mention to the mouse stores used by the Indians as food, and writing in 1845, Father De Smet says: 'The earth pea and bean are also delicious and nourishing roots found commonly in low and alluvial lands. The above named roots form a considerable portion of the sustenance of these Indians during winter. They seek them in places where mice and other little animals, in particular the ground squirrel, have piled them in heaps.'

"The extent to which these beans have been used by the Indians as food is evidently greater than has been generally supposed. Some of the Dakotas at Cannon Ball, North Dakota, have told me of gathering several bushels each autumn from the mouse stores, and both Indians and whites greatly prize them as a rich and delicious food. They are large, fleshy beans produced on underground shoots of a trifoliate bean vine, *Falcata comosa* [*Amphicarpa monoica*, or hog peanut].

"The artichokes stored with the beans are the tubers of a wild sunflower (*Helianthus tuberosus*) also growing abundantly on the rich bottomlands of the river valleys. They, too, are a valuable food, and much used by the Indians, and are gathered from the ground where they grow as well as from the mouse collections."

An Illinois burrow of *Microtus ochrogaster*, examined in November, is described by Kennicott ('57, p. 99) as follows: "The nest was placed near the centre of the burrow; and at one side and in the deepest part of the excavation, was the store of winter provisions. This consisted of five or six quarts of roots, chiefly the round

tubers of two species of spike-flower (*Liatris*), which grow abundantly in the vicinity, with a few roots of *Helianthus*, and of various grasses, and several bulbs of wild onions." Nelson ('18, p. 406) adds: "Some of the northern mice, however, gather stores of food for winter. A species [*M. operarius*] living along the coast of the Bering Sea and elsewhere on the Arctic tundra of Alaska accumulates a quart or more of little bulbous grass roots, which are delicious when boiled. They are hidden in nests of grass and moss among the surface vegetation, and before the first snowfall I have seen the Eskimo women searching for them by prodding likely places with a long stick. The roots thus taken from the mice are kept to be served as a delicacy to guests during winter festivals."

An important factor in the origin of plagues among *Microtus arvalis* of France has been their habit of building magazines for food storage (Regnier and Pussard, '26c, p. 92). These stores sometimes surpass three kilograms in weight, and there may be two or three within a short distance of one nest. Their presence during the winter constitutes one of the important factors in the ability of the voles to increase their population rapidly. These winter reserves that help tide them over the unfavorable season are composed chiefly of rhizomes, bulbs and roots of "noxious" weeds. They supply a type of food (vitamin X) which the authors believe to be important at the outset of a breeding period.

Stores of the Pine Mouse. Young sprouts of white clover, (*Trifolium repens*) the fruit of the red-haw (*Crataegus coccinea*) and the tuberous roots of the wild violet (*Viola cucullata*) are listed by Quick and Butler ('85, p. 116) as among food materials stored underground. They write (*loc. cit.*) that these deposits sometimes contain a gallon of tubers and extend eighteen inches below the ground. Kennicott ('57, p. 103) records that the acorns of the burr oak and white oak formed most of the stores which he examined.

Stores of the Red-backed Mouse. Bailey ('97, p. 116) says that he has never found evidence of these voles storing provisions, though later, ('26, p. 89) he states that they may be one of the "bean mice" of the Missouri River region.

Stores of the Lemming Vole. According to Quick and Butler ('85, pp. 114-115), "Cooper's mice live in winter chiefly upon the stems of blue grass and the more tender portions of the white clover. Stores of these foods may be found near their winter quarters. In November, 1883, a large quantity of the tuberous roots of the plant commonly called 'wild artichoke' (*Helianthus doronicoides* Lam.) were found in one of the storehouses of a colony of these mice."

TIME OF ACTIVITY

Observers agree that the four microtines here considered remain active the entire year, regardless of temperature.

Though up and around at any hour of the day, *Microtus* is chiefly nocturnal. The red-backed mouse, too, is active day and night, though in my experience more diurnal than the meadow mouse. The pine mouse is commonly said to be the most diurnal of these three. Burt ('28, p. 216) states that the lemming vole is chiefly nocturnal, though it is not uncommon to see it running about in the day time, either in the laboratory or in the field.

SOCIAL TRAITS AND DISPOSITION

The Meadow Mouse. The meadow mouse is usually found in colonies. Their runways and tunnels seem to be the work and property of the community at large, while stores apparently are shared by at least several individuals. This then shows a social condition above the mere gregarious association of many mice in one suitable area.

Bailey ('24, p. 527) has best summed up their behavior when he wrote of them: "In their own families and among their own friends meadow mice are generally friendly, playful, and even affectionate, but there are times when with strangers, rivals or intruders they are vicious little savages. The mother will fight anything from another mouse to a bulldog or a man in defense of her young. Possession of a cage, a nest, or a favorite corner is sometimes the cause of a quarrel, of squeaky disputes, or even a fight in which the intruder generally yields and retires. . . . The real fights are among rival males and usually males from different families, and these are apt to be serious or sometimes fatal. One nearly fullgrown male that by mistake was dropped into the cage with an older and larger male was nearly killed in a few minutes before it could be rescued. Both fought savagely and so fast that their motions were a complete blur, so that nothing could be seen of their methods of attack. When separated, the smaller one was found to be so badly injured that he was killed and his skin and skull saved for a specimen. He was bitten around the head, on the back, belly, feet, and tail, two large gashes were cut across the abdomen, and the skin of the back was so full of holes that it looked like a shotgun target. He would have been killed in a very short time if left in the fight. The larger male

seemed stiff and sore for a few days, but recovered from his injuries. Occasionally, a male is trapped in the meadows with his skin cut full of holes from a fight, in which case he may be safely assumed to be the sole survivor of a fatal combat." And further, pp. 525-526: "There is great individuality, however, in dispositions and habits, some mice being comparatively timid and nervous, while others are more gentle and confident, seeking rather than avoiding notice. Some are very fond of certain foods which others have not learned to like or will not eat. Some individuals are very talkative, always squeaking or making some noise at the others, while more of the individuals are quiet and generally silent. Some are far more pugnacious than others and often bite if handled, while others may be held in the hands and stroked without offering any resistance. These differences are noticed in the young just beginning to run about, and seem to be to some extent inherited characteristics."

The Pine Mouse. In regard to this species (which he calls "meadow mouse"), Kennicott writes ('57, p. 103): "This is the smallest of our rodents, and, for its size, I know of no mammal more pugnacious than the males, at least. I placed one in a box with a specimen of *Sorex dekayi* [*Blarina brevicauda*], which it at once attacked. The shrew was courageous and never retreated, neither did he attempt to pursue the other to any distance. The meadow mouse acted on the offensive, and made unprovoked attacks, the cage being large enough for both. He approached the shrew cautiously, and when within two or three inches sprang upon him, biting and striking with his feet, and then jumping back quickly, in fact fighting in the same manner as the *Arvicola austerus* [*Microtus ochrogaster*]. When he came near, and the shrew made the first attack, the meadow mouse would rise upon his hind feet, and strike with his fore ones, and snap rapidly with his teeth. Had the fight been allowed to continue, it is probable that the shrew would have been beaten; for, though much the stronger, and doubtless able to kill the meadow mouse readily, if he could grapple with him, the latter was enabled, by his sudden springs, to inflict severe wounds and exhaust his adversary, without being much hurt himself. The shrew constantly uttered his sharp bird-like twitter; but the meadow mouse fought in silence."

The Red-backed Mouse. Red-backed mice, like meadow mice, are more or less colonial, but to what extent they are social I do not know. Some pairs which I have kept together for varying periods fought a great deal, others lived peacefully together for several months. In all probability they possess about the same social traits as their meadow living cousins.

The Lemming Vole. Burt ('28, pp. 215-216) writes of this animal: "The lemming mice seem to be of a nervous temperament. Twice pregnant females that showed no signs of injury were brought into the laboratory, only to die shortly after arriving. As a rule the mice are slow and cautious in their movements, but when frightened can move rapidly. They can be handled with ease, and once in the hands show no sign of fear. Very seldom do they offer to bite the person holding them."

INTERCOMMUNICATION

Meadow Mouse. Bailey ('24, p. 525) writes: "Meadow mice are by no means dumb, as some have asserted, though to our gross ears they may seem so. The young have many forms of minute whimpering, whining, crying sounds which seem to have a meaning to their mother. As she leaves the nest, and perhaps interrupts their meal, there is a fine little complaining jumble of whimpers from the very young, to which she pays no attention. If one tumbles out of the nest and lies wriggling helplessly on the floor it cries with a vigor that brings a quick parental response and is carried back and replaced in the nest. If it falls far enough to be slightly hurt, but not to be greatly injured, a sharp squeal of pain sets the mother frantic to find and help it.

"The adults and the older young have little talky squeaks and sharp cross squeaks and savage squeals, and in a fight a blur of squeaks and squeals and guttural growls, not far different from a dog fight on a very small scale. Then there are chatterings of teeth at each other and stampings and scratchings on the ground when rivals meet, all of which, and probably much more that we miss, have an evident meaning to them. A stranger or friend is recognized, either by voice, odor, sight, or other token, as quickly as we recognize a friend or foe."



Fig. 168. Dry pastured field, Bedford, N. Y. Grazing and aridity are responsible for keeping meadow mice from such a field as this.



Fig. 169. Fields, Bedford, N. Y. The fields in the extreme distance that are unpastured support a meadow mouse population. Those in the foreground and to the right are uninhabited.



Fig. 170. Mouse runways in a small dry field exposed by burning. The grass here had not been cut in three years, and the mice did great damage in the nearby garden. Bedford, N. Y.



Fig. 171. Excavated earth marking the course of burrows used by meadow mice in a Bedford, N. Y., marsh.

The hip glands on the males will, when some one takes up the problem, doubtless be shown to subserve some function of intercommunication. Their position is favorable for leaving an odor on the vegetation that flanks their runways, or on the earth sides of the burrows. It is not likely that the glands are under control of the will. From being limited to the adult male, one would judge that they served somehow in bringing the sexes together.

Many animals appear to signal by stamping with fore or hind feet or by drumming with the digits. I have not observed such action in *Microtus*, but it is something that may be looked for by anyone who has ample opportunity to watch this animal.

Pine Mouse. According to Kennicott ('57, p. 103), "This species, in fact, is always much more silent than the . . . [meadow mouse]. When hurt, however, it utters a low cry, softer and shorter than that of the *Arvicola austerus* [*Microtus ochrogaster*]."

Red-backed Mouse. The only sounds which I have heard this mouse utter were series of high pitched "mouse-like" squeals. These were most commonly heard when the mice were fighting.

Odor glands occur on each flank of the adult males. These form prominent spots, about a half inch in diameter, on which there is a dense growth of hair. Doubtless their function is the same as that of the similar glands of *Microtus*.

Lemming Vole. I find no record of the voice of the lemming vole.

DESTRUCTIVE AGENCIES OF VOLES

The meadow mice are rapid breeders, and in consequence have many enemies—or did the enemies come first and the rapid breeding-rate afterwards? At least, we know that when these various agencies of control—weather, fire, disease, and predacious animals, ease up in their effect, the mice may attain a supremacy that is not good for them as individuals—or for their associates.

The Value of Vertebrate Enemies of Mice. Though it is incontestable that snakes, birds and carnivorous mammals carry on a constant warfare against meadow mice, it is not universally con-

ceded that this destruction is of paramount importance in the control of the small rodent populations. Seasonal conditions, the absence of shelter and food and the acts of man are often advanced as controls of so much greater magnitude that the effectiveness of the predatory species is overlooked.

That these natural enemies are unable to cope with an actual plague once it has gotten well under way, has been demonstrated in several outbreaks, yet on the other hand, how many potential plagues have not undoubtedly been frustrated in their early stages by these natural destructive agencies of mice? It is difficult to obtain a fair view of the facts for different observers of the same field conditions give sharply contrasting pictures of the situation. Thus in reference to the Buena Vista outbreak, Wyman ('27, p. 142) wrote: "In this Buena Vista Lake region, as in all California, hawks and owls have been killed almost to extermination, with practically no interference by the officials whose duty it is to enforce laws provided for the protection of such birds; while the four-footed mouse-eaters as coyotes, skunks and badgers, are as systematically persecuted. Had these control factors existed in their natural numbers, the increase of mice would have brought them to the spot in thousands, and the plague would have been nipped at its inception. Once out of bounds, the pitiful remnant of the mouse-eating forces is a mere onlooker at a spectacle which illustrates the folly of man in tampering with Nature's well organized machine."

Hall ('27a, pp. 199-201), though agreeing on the lack of mammals, gives a different picture as to the numbers of birds present: "Hawks, owls, and ravens were more abundant here than usual. This statement is made both on the basis of reports of local residents, and on the writer's own personal field observations here as compared with those in similar localities where mice were not overly abundant. Named in order of their abundance from first to last, the hawks noted were: Marsh Hawk (*Circus hudsonius*), Western Red-tailed Hawk (*Buteo borealis calurus*), Desert Sparrow Hawk (*Falco sparverius phalaena*), and a rough-legged hawk (*Archibuteo* sp.?). Barn Owls (*Tyto pratincola*) were abundant and Short-eared Owls (*Asio flammeus*) were seen wherever there was terrestrial cover, a condition that obtained only at the eastern end of the lake. . . .

"Although predatory birds were abundant, predatory mammals were extremely rare in the infested area. In fact I saw none, nor

even any sign, such as tracks, droppings, and inhabited burrows. In similar territory where normal numbers of coyotes, kit foxes, striped skunks, spotted skunks, badgers, and weasels occur, one would, in doing the same amount of field work that I did here, see signs of the animals on numerous occasions and probably some of the animals themselves. Reports of residents of the region when questioned on this point, were without exception to the effect that the above mentioned mammals used to be frequently noted, but not recently. When questioned as to the length of time this scarcity had been evident, the replies usually were: 'I haven't seen any for two years.' Some times the time was given as 'about a year and a half.' As to the cause of this scarcity of predatory mammals, the people questioned ascribed it to the fact that the animals mentioned had to have water and consequently left after the lake had been dry for a while, or to unknown causes. As a matter of fact, water was available in sloughs and irrigation ditches, and the drying up of the lake would not account for the disappearance of all carnivores.

"Naturally puzzled at this apparent absence of these predatory enemies of the mice, the writer kept careful watch for any evidence of them, but no carnivorous mammal, or sign of any, was found. Subsequently it was learned that an intensive campaign against the coyotes of the region had been waged under the auspices of a federal bureau in the winter of 1924-25, at the request of, or at least for the assumed benefit of, sheepmen, since the coyotes and bobcats take toll of the flocks at certain seasons. The campaign was carried on by generously distributing poisoned baits over the country. Known results of the campaign are indicated by the following sample observation made shortly after the time it was being carried on. 'For instance, near Buena Vista Lake (I am assured that this was within two miles of the lake), in January, 1925, in a distance of one mile along a road, 5 skunks and 2 coyotes were found dead. In this locality, 25 skunks, 8 coyotes and 7 kit foxes were found dead by Arthur Oliver, the evidence being conclusive that they had been killed by poison set out for coyotes. In general it was found that the poison campaign was terribly effective; perhaps more so to kit foxes and skunks than to coyotes' (field notebook in Museum of Vertebrate Zoology)."

Brooks ('27, p. 249), on the other hand, in regard to this same phenomenon wrote as follows: "Hawks were especially plentiful

and a few were seen lying dead by the roadside, the victims of ignorant gunners, but only a few. At Snelling, Merced County, only some 180 miles north of the region where the mouse plague occurred in the latter part of 1926, hawks were more numerous than I have seen them at any point in North America in the last forty-six years. . . . On January 2, 1923, just four years before the height of the mouse plague I counted 120 hawks of the *Buteo* type in the air at once. This was not a migrating assemblage, but just a normal concentration near a roosting point. Redtails constituted the majority of this gathering. Ferruginous Rough-legs, the 'notably scarce or altogether wanting' California Squirrel Hawk, were well represented, and a few Red-bellied Hawks completed the list. All of these are notable mouse catchers and in addition Marsh Hawks and Sparrow Hawks were abundant and seen at all points in the San Joaquin and Sacramento valleys.

"Owls of several species were also numerous as well as coyotes, skunks, 'coons and weasels. [This was before the Federal poisoning operations.] In fact never in my life have I seen such a notable abundance of mouse catchers, including feral domestic cats in extraordinary numbers. Yet only four years later comes this devastating plague of rodents!"

Piper ('28, pp. 550-552 and 560) recorded the gathering of ring-billed gulls, short-eared owls, and ravens, but concluded that though the work of the preying species was impressive, obviously it was insufficient either to prevent or to end the extraordinary increase.

All the chroniclers of this California outbreak agreed, as have those who described earlier plagues, that there was an undue destruction of hawks and owls by misinformed farmers in the invaded district. Such shortsightedness is, of course, common with regard to flesh-eating species against which popular prejudice is strong.

Aside from their unmeasured value as plague checks, the birds and mammals are constant and important controls in ordinary times over large areas. The birds are generally credited with the more important role, for in their castings, in their more generally observed hunting movements, and in the more complete reports of stomach contents, their microtine food is documented and appreciated by those who trouble themselves to look for the truth. Mammals, on the other hand, hunt more generally by night, and are inconspicuous in

their movements. They do not leave such easily recognizable records as the castings of owls and hawks. Their stomach contents have not been so well studied. For all we know, they may, where they are not too limited in numbers, kill more voles than do the raptorial birds.

It is rather strange that instead of protecting our greatest agricultural friends we persecute them relentlessly. Notwithstanding the fact that it is demonstrated that the majority of the hawks and owls are mainly or entirely beneficial to the farmer, there are few laws protecting them, and these few are largely unenforced. Most farmers shoot on sight any hawk or owl that they see and thus open up the way for many troubles. If a hen is carried off, every hawk that closely or remotely resembles the culprit is shot as a matter of principle, if the opportunity presents itself.

Sportsmen even go so far as to offer bounties and prizes for the destruction of alleged "game-destroying" birds and mammals. Lantz ('07, p. 38) records and comments on one such case: "Nine competitors for a club's prizes destroyed during twelve months 184 weasels, 48 foxes, 54 minks, 343 skunks, 15 great horned owls, 6 'common owls', and 148 hawks. The fact that only 21 owls were killed in an entire year by nine men trying for a record reveals a scarcity of these useful birds that is not complimentary to the intelligence of the community. The large number of skunks killed indicates ignorance or disregard of the usefulness of that animal in destroying insects and mice. Apparently, too, there was no discrimination as to the species of hawks destroyed, and it is probably safe to say that field mice in a single year have damaged the farmers of the regions concerned a hundredfold more than the value of all the game and poultry saved through the offer of prizes."

Quoting Buckland, ('14, p. 451): "In 1885 the Legislature of Pennsylvania passed an act, known as the 'scalp act' which provided a bounty of 50 cents each on hawks and owls killed within the State limits, and a fee of 20 cents to the notary taking the affidavit. As the results of this act \$90,000 was paid in bounties during the year and a half subsequent to the passage of the act. An irruption of small rodents followed and did damage to the agricultural interests of the State amounting to \$3,850,000. And even these figures . . . do not represent the entire loss. Years must elapse before the balance of nature which was destroyed, can be restored."

We can only hope that wide circulation of the facts may some day overcome the current blind prejudice fostered and transmitted from one generation to the next merely because of the occasional farmyard depredations of a very few species of birds and mammals. The records quoted have certainly demonstrated the fact that our common birds and mammals feed so generally on mice that we should encourage their increase for this one reason alone, even if there were nothing else to be said in their favor. Let us review the various vertebrate animals that help to hold the mouse population within normal bounds.

Amphibians. BULLFROG (*Rana catesbeiana*). The bullfrog is commonly credited with doing his bit towards making the world safe for farming by eating meadow mice. I even find an actual record of a *Microtus* taken from one of sixteen stomachs examined at Saranac Inn, New York (Needham, '05, p. 12).

Reptiles. BLACKSNAKE OR BLUE RACER (*Coluber constrictor*). Meadow mice form a large part of the food of the blacksnake—22 per cent of a series examined by Surface ('06, p. 169). In the New York region I have seen more of these snakes in meadow mouse habitats than in any other situation.

PILOT SNAKE (*Elaphe obsoleta*). This snake is also known to take meadow mice. Hay ('92, p. 503) cites this fact, and Surface ('06, pp. 160–163) records *Microtus* from their stomachs to the extent of ten per cent of the total, reaching 37½ per cent in August and September.

FOX SNAKE (*Elaphe vulpina*). The fox snake feeds largely on small rodents. Kennicott ('57, p. 88) records meadow mice as among their prey and Ditmars ('07, p. 297) mentions simply "mice."

BULL SNAKE (*Pituophis sayi*). Lantz ('18a, p. 11) writes that this western snake eats meadow mice.

MILK SNAKE (*Lampropeltis triangulum*). There are records of meadow mice taken from stomachs of this snake, and a wide variety of other small animals is included in the list of species eaten (Cope, '00, p. 886, and Kennicott, '57, p. 88). Surface ('06, p. 178) found meadow mice constituting 48½ per cent of their food and in September and October rising as high as 67 per cent.

WATER SNAKE (*Natrix sipedon*). The water snakes are apparently occasional eaters of mice, though fish constitute the bulk of their food. Surface ('96, p. 156), for example, records *Microtus pennsylvanicus* from one stomach. It is possible, however, that meadow mice when eaten are taken as carrion.

GARTER SNAKE (*Thamnophis* spp.). Kennicott ('57, p. 99) writes: "Mr. Job Galloway, of Northfield, informs me that, while mowing in a low prairie, inhabited during summer by this species, he observed a small garter snake passing rapidly through the grass, with a young meadow-mouse, partly swallowed, in its mouth. The low squeak uttered by the latter attracted his attention. Presently, an old meadow-mouse emerged from the tall grass in pursuit of the snake. Stopping an instant, as if to listen for the cry of her young, she again pursued, and finally overtook the snake, which she unhesitatingly attacked. The snake stopped, disgorged his prey, and defended himself by striking at his assailant, which appeared to be beating him, when he was killed by Mr. Galloway."

Kennicott (loc. cit., p. 88) further states that "Meadow-mice are also devoured by the common large-striped, or garter-snake (*Eutaenia* [*Thamnophis*] *sirtalis*) and are undoubtedly eaten by another garter-snake (*Eutaenia* [*Thamnophis*] *radix*) which is our most abundant reptile on the prairies." Personally, I believe that mouse eating garter snakes are rare, at least I have never taken one, and the white-footed mice which I caged with a garter snake ate the snake!

COPPERHEAD (*Agkistrodon mokasen*). Of the food of copper-heads listed by Surface ('06, p. 188), 23½ per cent consisted of "field mice".

RATTLESNAKES (*Crotalus* and *Sistrurus*). Says Kennicott ('57, pp. 87-88): "*Arvicolae* are the legitimate food of the prairie rattlesnake or massa sauga. In many specimens of this snake examined, I have not found one the stomach of which did not contain the remains of Meadow-mice. The rattlesnake can readily enter their burrows, and is certainly more or less nocturnal; so that the *arvicolae* [*Microtinae*] when out at night, fall an easy prey to this voracious reptile, which, though noted for its ability to endure wonderful fasts, even of a year or more, in captivity, is, never-the-less, a huge feeder naturally. I have taken the partly digested bodies of 5 adult *arvicolae*, with the remains of two small garter-snakes, and some bird's feathers, from the stomach of a rattlesnake; and have repeatedly found the remains of several mice in various stages of digestion in the stomach of one of them, showing that they had been caught at different times. And, I would here remark, that I have little faith in the opinion popular among farmers that rattlesnakes eat only at long intervals from choice. Observations indicate the contrary."

Taylor ('92, p. 357) also credits the rattler with being chiefly a mouse feeder. Surface ('06, p. 196) found meadow mice constituting 37½ per cent of the food of *Crotalus horridus*.

SNAPPING TURTLE (*Chelydra serpentina*). Surface ('08, p. 129) records mice in two of nineteen snapping turtle stomachs examined. Probably these were meadow mice, which are doubtless often exposed to attacks by snapping turtles in their own habitat.

Birds. The following species are mentioned in the literature as among the enemies of voles, but the extent of their activities in this respect varies greatly. Some can hardly be said to be more than occasional and perhaps more or less accidental feeders on these rodents, others prey upon them sufficiently to be classed as natural enemies of some importance.

LONG-TAILED JAEGER (*Stercorarius longicaudus*). Bent ('21, p. 25) writes that in their summer home on the tundra these jaegers feed largely on lemmings, *Microtus*, and other small mammals.

IVORY GULL (*Pagophila alba*). An indiscriminate feeder preying to some extent on mice, according to Bent ('21, p. 33).

CALIFORNIA GULL (*Larus californicus*). This gull in times of mouse outbreaks has been known to feed upon these pests. Bent ('21, p. 129), quoting Dutcher, records the following interesting letter by Mr. John E. Cox of the Utah Board of Agriculture: "Gulls go all over the State for insects, the greatest number visiting the beet fields, where they keep down the crickets, grasshoppers, cutworms, etc. They took a new diet this summer. Some alfalfa fields were so badly honeycombed with nice holes and runs that it was impossible to irrigate them, and they were plowed up, mostly for beet culture. When the water was turned into the irrigation ditches, the mice were forced out of their holes, and the gulls then caught them. They became so perfect in their work that they kept abreast of the head of the water and picked up every mouse that appeared. When gorged with victims they would vomit them up in piles on the ditch bank and recommence their feeding. Gulls are sacred in Utah, and are so tame that oftentimes they may be caught by hand as they follow the plow so closely.'"

RING-BILLED GULL (*Larus delawarensis*). Said to do efficient work in killing *Microtus*, particularly in times of excessive numbers. This has been attested by several observers.

WOOD IBIS (*Tantalus loculator*). According to Lantz ('07, p. 52), this is another enemy of the meadow mouse.

AMERICAN BITTERN (*Botaurus lentiginosus*). Again quoting Lantz (loc. cit.): "Of our herons, the American bittern is probably the best known destroyer of voles. The bird is a summer resident in all suitable localities in temperate North America, making its home



Fig. 172. Three nests of meadow mice, unusually close together. Bedford, N. Y. April 27, 1929.



Fig. 173. A nest of *Microtus*, lifted from its site. Bedford, N. Y. April 27, 1929.



Fig. 174. A typical nest of *Microtus*, Bedford, N. Y. April 27, 1929.



Fig. 175. *Microtus* nest in the center of a hummock. Bedford, N. Y.

in moist meadows, bogs, and swamps. Baird, Brewer, and Ridgway say of it: 'It does not move about much by day, although it is not strictly nocturnal, but is sometimes seen flying low over the marshes in pursuit of short-tailed or meadow mice, which are frequently taken whole from its stomach.' Records of the Biological Survey contain a number of instances in which meadow mice were found in stomachs of this species."

LEAST BITTERN (*Ardetta exilis*). Feeds occasionally on meadow mice (Lantz, loc. cit.).

GREAT BLUE HERON (*Ardea herodias*). The great blue heron hunts in marshy places where meadow mice live and it is often said that the bird feeds upon these mice. Fisher ('09, p. 193) writes that pellets collected at an inland nesting site indicated that the young were fed largely on small rodents.

AMERICAN EGRET (*Herodias egretta*). Also eats meadow mice (Lantz, '07, p. 52).

SNOWY HERON (*Egretta candidissima*). Meadow mice are among the things eaten (Lantz, loc. cit.).

BLACK-CROWNED NIGHT HERON (*Nycticorax nycticorax naevius*). Meadow mice are also listed among the food of this bird (Lantz, loc. cit.).

SANDHILL CRANE (*Grus canadensis*). Kennicott ('57, p. 87): "A domesticated brown sandhill crane, which I kept for several years, spent much time in hunting about the fields for the nests of Meadow-mice. He became expert in finding them, and when they were situated upon or near the surface he would dig them out with his long and powerful beak, and after first killing all the inmates, proceed to swallow them whole, with much apparent relish. In spring I have seen him thus destroy several families of old and young *arvicolae* in a day. Cranes are carnivorous and large feeders, and if all are as good mouse-catchers as my pet, they must destroy great quantities on the prairie."

MARSH HAWK (*Circus hudsonius*). The importance of our common hawks and owls as destroyers of the various species of "mice" is strikingly brought out in Fisher's ('93) well known investigations on the food habits of these birds of prey.

The marsh hawk, or harrier, is probably the most common and most widely distributed North American hawk. According to Fisher (op. cit., pp. 29-32), of 124 stomachs of this species examined, 57 contained "mice". Meadow mice were identified in 40 stomachs, averaging almost two to each. Eight were found in one stomach. The other mammals preyed upon were mainly other species of mice, ground squirrels and rabbits.

RED-TAILED HAWK (*Buteo borealis*). Red-tailed hawks, though perhaps not the most important of the hawks in mouse control, are frequent feeders on these small rodents. They commonly hunt over meadows and fields where these voles live. Of 562 stomachs examined by Fisher (op. cit., p. 62), 278 contained mice.

RED-SHOULDERED HAWK (*Buteo lineatus*). Of 220 stomachs examined (op. cit., pp. 64-70), 102 contained "mice"; 40, other mammals. At least 65 per cent of the food of the red-shouldered hawk consists of small rodents. Meadow mice, red-backed mice, and pine mice have been taken from their stomachs.

SWAINSON'S HAWK (*Buteo swainsoni*). Of 18 Swainson hawks' stomachs examined by Fisher (op. cit., pp. 76-79), 7 contained small mammals, one of which was a mouse. Throughout its summer range this species lives almost entirely on grasshoppers.

ROUGH-LEGGED HAWK (*Archibuteo lagopus sancti-johannis*). Doctor Fisher (op. cit., p. 91) examined 49 stomachs of this hawk, forty of which contained mice only. Of these forty, 27 had meadow mice only in them, the average number being three to each hawk. All these are winter records and probably are not representative of summer conditions, when these hawks are said to be largely insectivorous. Kennicott ('57, p. 87) records the following instance of hawks of this species living on meadow mice. "Dr. Hoy informs me that near Racine he observed, in autumn, a flock of black-hawks, 20 or 30 in number, to frequent a high knoll to which numerous Meadow-mice had been driven by the inundation of the surrounding lowlands. This they visited morning and evening for over a month, during which time they appeared to feed upon nothing else than Meadow-mice. One of them, shot late in autumn, was exceedingly fat, and had the remains of 4 full-grown *arvicolae* in his stomach. Dr. Hoy estimated the number destroyed by the flock in six weeks at over 8,000. He says that they form the chief food of this hawk in the West, and that it should be regarded as a friend to the farmer, the more so as it does not make predatory descents on the farm-yard."

SPARROW HAWK (*Falco sparverius*). Of 320 stomachs examined by Fisher, 89 contained mice. This is the commonest of our small hawks and its chief food is insects and mice.

BARN OWL (*Tyto alba pratincola*). The ranges of the barn owl and the meadow mouse overlap in an extensive area. That the bird preys upon the voles to a large extent is shown by several records. Fisher (op. cit., p. 139), in an examination of 39 stomachs of this species, found both meadow mice and pine mice. In an examination

of 1247 barn owl pellets, collected in the towers of the Smithsonian Building in Washington, D. C., he found 1991 skulls of voles, 656 of house mice, 210 of the Norway rat, and 147 of other small rodents and shrews (Lantz, '18a, p. 12).

At Berkeley, California, the barn owls feed principally upon *Microtus*, though also on many other small mammals. Foster ('26, p. 130 and '27, p. 246) and Hall ('27b, p. 274), who examined barn owl pellets from this locality, found that a combined total of 1407 individuals of *Microtus californicus* had been eaten, as against a total of 757 individuals of other small mammals, divided among 11 genera.

Hall has pointed out the important rôle that the barn owls, as well as cats, play here in protecting the city lawns by keeping down the mouse populations at the borders of the city.

LONG-EARED OWL (*Asio wilsonianus*). Pellets of this species from Windsor, Connecticut, which I examined, contained skeletal remains of 13 *Microtus pennsylvanicus*, but no other mammalian species. About 20 pellets taken in February, 1929, at Greenwich, Connecticut, contained remains of 65 *Microtus pennsylvanicus* and 4 *Blarina brevicauda*.

Of 107 stomachs examined by Fisher ('93, pp. 141-145), 84 contained microtines representing the meadow mouse, the pine mouse, the red-backed mouse and the lemming vole. About 50 pellets from long-eared owls contained 176 skulls, representing 95 meadow mice, 19 pine mice, 3 lemming voles, 20 other mice, 26 shrews and 13 birds.

In its range, this bird is probably the greatest microtine killer among the owls. Extensive counts of pellets of this species collected in New Jersey by W. DeW. Miller, show a heavy preponderance of microtines in the series, as well as a much greater percentage of microtines among pellets of long-eared owls than in pellets of other owl species. This may be due to a preference in taste for microtine flesh, but in some localities preponderance of microtine skulls could be accounted for by the greater abundance of the species in the owl's hunting grounds.

SHORT-EARED OWL (*Asio flammeus*). The short-eared owl occurs over a large section of the globe and is everywhere a mouse feeder. Time after time it has flocked to the scene of mouse plagues until the hordes of these rodents are decimated. Many such accounts may be found in the story of the Scotch plague (Maxwell, '93, p. 128, *et. seq.*).

Doctor Fisher reports the result of examinations of 101 stomachs. Of these 77 contained mice, among which 87 meadow mice were identified.

Short-eared owls were exceedingly numerous in the Yakima Valley during a mouse outbreak in 1922-1923, and probably were an effective aid to the campaign of eradication carried on against the mice at that time (Couch, '28, p. 74).

BARRED OWL (*Syrnium varium*). Of the 109 stomachs examined by Fisher (op. cit., pp. 154-156) 46 contained mice, more than half of which were definitely identified as meadow mice.

SCREECH OWL (*Otus asio*). The screech owl is probably the most familiar of American owls. Being too small to prey upon domestic fowl or game, it is, perhaps, in the main beneficial. Its habit of staying close to buildings and in orchards makes it particularly useful about farm buildings. Doctor Fisher (op. cit., p. 173) reported on the contents of 255 stomachs, of which 91 contained mice, about a third of which were identified as meadow mice, and 24 as house mice.

GREAT HORNED OWL (*Bubo virginianus*). Where such are available great horned owls possibly feed more on rabbits and other game larger than mice. Fisher (op. cit., p. 182), who examined 127 stomachs of this owl, found meadow mice of several species in 13 of them.

SNOWY OWL (*Nyctea nyctea*). According to Couch ('28, p. 74), snowy owls aided materially in controlling a mouse outbreak in Okanogan and Wenatchee Valleys, Washington, during the winter of 1922-23.

CROW (*Corvus brachyrhynchos*). The food habits of crows have been carefully studied by Barrows and Schwarz ('95, pp. 29-35). They found from an examination of 909 stomachs that only about 1 per cent of the food through the year consisted of mice (78 stomachs), though in March this rose to $3\frac{1}{2}$ per cent. Mice rank fourth in order of importance on the list of animal food for the year, though about half of those eaten are in the form of carrion.

Crows search out the nests of meadow mice at all times of the year. When their own young are in the nest the birds are particularly active in mousing, taking both the adults and the young. In winter the crows are said to search for the small holes in the surface of the snow, that are caused by the heat arising from the inhabited mouse nests beneath the surface.

The crows, staying on through the year in larger numbers than do most of the other bird enemies of meadow mice, constitute a beneficial agency to man that should not be overlooked or considered too lightly.

"It is of interest," writes Lantz ('07, p. 51), "to note that complaints of recent depredations of field mice are especially numerous

from sections of the United States where for several years past bounties have been paid for killing crows."

RAVEN (*Corvus corax*). Ravens feed extensively on mice and in certain parts of the country may often be seen in cultivated areas feeding where mice are common.

NORTHERN SHRIKE (*Lanius borealis*). Says Lantz (op. cit., pp. 51-52): "It comes to the United States at a time when insects are not abundant, and feeds mainly upon small birds, mammals, and grasshoppers. Mice were found in one-third of the stomachs examined by the Biological Survey and more than half of those identified were meadow mice. Doctor Mearns is quoted as authority for the statement that in Minnesota during March, shrikes live almost exclusively on meadow mice. Most farmers have noticed that the northern shrike, or 'butcher bird' catches meadow mice. The birds are often seen at husking time as they hover in the air or sit on a fence post or top of a hedge, ready to pounce upon every mouse that escapes from corn shocks as they are torn down or moved.

"The smaller shrikes (*Lanius ludovicianus* and subspecies) also somewhat resemble mocking birds in color. They are summer residents of many parts of the United States. As insects are abundant during the greater part of their stay, they are insectivorous to a greater extent than the northern shrike. Stomach examinations prove that mice form 16 per cent of the food for the entire year, but the birds are less able than the larger species to cope successfully with adult meadow mice, yet they undoubtedly destroy a good many voles, and several have been identified in their food; but smaller mice are more frequently caught."

Kennicott ('57, pp. 86-87) writes thus: "One of their greatest enemies in this vicinity [West Northfield, Ill.] is the northern shrike, or butcher-bird, the food of which consists almost wholly of *arvicolae* and a few prairie White-footed Mice, during his sojourn with us, in his spring and fall migrations. . . . The result of the shrike's watchfulness and prowess may be seen, in part, in the bodies of the numerous mice, fastened in the branches of bushes or on fences, sometimes partly eaten, sometimes having only the brains taken out, but oftener entire. Considering what he has devoured, besides these, the large numbers destroyed by the shrike may be readily supposed. The southern shrike, which breeds largely in the prairie districts throughout this State, is also an enemy to be dreaded by the Meadow-mice. Though feeding more upon insects than its larger cousin, and being, perhaps, a less successful mouser, its destruction

of *arvicolae* in summer is well-known, and has gained for it the name of 'mouse-bird' in central Illinois. This bird not only pounces upon them when they are moving about, but finds the nests on the surface, and digs out the inmates with its bill and claws."

MAMMALS. OPOSSUM (*Didelphis virginiana*). The opossum hunts and kills meadow mice and in its range is doubtless more or less important as a control animal; yet being one of the most nearly omnivorous of our mammals it does not specialize in mouse hunting but takes whatever lies in its path.

SHREWS (*Blarina* and *Sorex*). "That shrews," says Lantz ('07, p. 41), "destroy many field mice is certain, although the evidence is largely circumstantial. It is known that they eat dead mice that have been caught in traps. It is proved that they are able to capture a live field mouse in its burrow by the fact that when both animals are confined in the same cage the shrew kills and partly eats the other animal. Shrews are often trapped in the burrows of field mice, and it is highly probable that they habitually feed upon the rodents. As they eat only the flesh and blood of their victims it is difficult to identify their food by stomach examination."

A pine mouse which Kennicott ('57, p. 103) placed in a cage with a *Blarina* threatened to reverse the order of things for it took the offensive and by superior agility, for the time had the better of the fight.

BEARS (*Euarctos* and *Ursus*). The bears eat anything they can get, and in the list, of course, are mice. I have no definite record of bears destroying voles but it is commonly believed that they are not above eating such small fry when opportunity offers. Where bears occur there is not much agricultural activity and hence no crops to be injured by voles, so we can only put bruin in the old picture of Nature's balance, without being able to say that he is part of the army of wild things that protects the farmer against a host of his generally unseen foes.

RACCOON (*Procyon lotor*). Like the bear, the raccoon does not refuse the luckless mouse that chances in its path. The 'coon is not an habitual hunter of voles, but in its hunting in the wet places many nests of meadow mice doubtless are found and emptied of their tenants. Lantz ('18a, p. 11) definitely recognized the raccoon as a destroyer of meadow mice.

MARTEN (*Martes americana*). The marten is by habit said to be a squirrel feeder above all else, but Seton ('09, p. 918) holds that its food supply rests chiefly on mice.

WEASEL (*Mustela* spp.). The weasels are efficient checks on the hordes of meadow mice. I have trapped them in *Microtus* runways, and have seen them in and near habitats which harbored meadow mice. They are, it is certain, among the most persistent destroyers of mice and are particularly valuable near human habitations, as they are less likely to be driven away from civilization than are most other mouse enemies. Active the entire year, they leave behind them a bloody trail of mouse left-overs during the period of their adult life. The smaller weasels are very probably the better mousers, for they may pursue mice in burrows too small for other carnivorous enemies to enter.

MINK (*Mustela vison*). It is said by Fisher ('09, p. 190) that the mink is indefatigable in its search for meadow mice. These mice evidently furnish more easily obtainable food than do fish and the muskrat, for example, which are other important items on the mink's bill-of-fare.

SKUNK (*Mephitis* and *Spilogale*). The skunk is a destroyer of *Microtus* at the most important season (Shaw, '28, p. 75) namely in the spring, at a time when the snow is disappearing and until the time when insect food becomes abundant. It is at this season that the mouse population is at its lowest ebb, yet is at the onset of its period of greatest breeding activity. Other mice also are eaten by skunks, but *Microtus* heads the list. Doubtless the greatest aid to farmers that a skunk accomplishes is its destruction of the meadow mice, although it eats quantities of grasshoppers and other harmful insects. Being able to withstand the inroads of civilization fairly well, the skunks fortunately have maintained their importance over a large area of the country.

In his "Economic Value of North American Skunks," Lantz ('17, pp. 13-14) gives the opinion that "Although other mammals, including coyotes, badgers, foxes, minks, and weasels do far more good by destroying noxious rodents than is generally realized, the skunk surpasses them all. It is sufficiently numerous in many localities to keep field mice in check, and reports from various parts of the country show that close trapping of skunks and other fur animals is often followed by an increase in depredations by mice. C. W. Douglas, nurseryman of Waukegan, Illinois, writing to the Biological Survey in 1906, attributed the abundance of meadow mice in that vicinity directly to the scarcity of skunks, weasels and other natural enemies. . . . The little spotted skunks are remarkably efficient as destroyers of rats and mice. They are small and nearly like a weasel in shape; they are quick in their movements, and can follow rats and mice into smaller crannies than the ordinary skunk can enter."

When some individuals take to raiding poultry houses it would appear better economy for the poultry keeper to make his buildings skunk proof rather than to kill the animal. The skunk may be worth many times as much alive as it is dead, at least in some situations.

Dixon ('25, pp. 43-45) found that in a series of California skunks, "harmful" mammals constituted 16.3 per cent of the bulk of their stomach contents; harmful insects, 24.9 per cent; and waste material (soil, parasitic worms, and vegetation), 37.5 per cent. He summarized his results with the statement that 68 per cent of the skunk's food was of beneficial significance, 27 per cent neutral, and 5 per cent harmful.

BADGER (*Taxidea taxus*). Where the badger occurs it is an important feeder upon *Microtus*.

"Badgers", says Lantz ('07, p. 40), "when not employed in unearthing larger rodents, devote much time and labor to digging out field mice. One will patiently excavate every burrow on an acre or more of ground, and, besides the litters of young, evidently get a large share of the old mice. Badgers have been caught with their intestines full of pellets of fur and bones of *Microtus*. Nevertheless, while doing almost no harm and while in general highly beneficial, badgers are destroyed almost everywhere, partly for sport, partly because on rare occasions one raids an unprotected chicken coop." Personally, I have found the chief complaint against the badgers in the West to be that horses are more or less likely to break their legs in their holes.

RED FOX and GRAY FOX (*Vulpes fulva* and *Urocyon cinereoargenteus*). The foxes constitute important members of the fraternity of mouse destroyers. They function particularly well in the drier situations. I have on several occasions seen them in places where *Microtus* lived. Of their food habits, Lantz ('07, pp. 40-41) has written:

"Foxes destroy many field mice and other rodents as well as many insects, especially grasshoppers, and thus do much to compensate for the poultry and game they kill. Although reliable testimony to the destruction of domestic fowls by the red fox is not wanting, the habit is by no means common, as is shown by the contents of stomachs examined by the Biological Survey. In three cases remains of the Gambel partridge were found and in one other a small bird. On the other hand, harmful rodents, including field mice, were found in over 20 stomachs. Besides these, a mole, a lizard, grass, corn, blueberries, and cultivated grapes show a somewhat miscellaneous diet. A writer in Forest and Stream states that in the stomach of a



Fig. 176. Sloop Island, Lake Champlain, N. Y., occupied by seven *Microtus*. August 23, 1926.



Fig. 177. Small apple tree girdled by mice that flourished in the uncut grass nearby. Bedford, N. Y.



Fig. 178. Hummock, the site of a meadow mouse nest containing young. This hummock is completely surrounded by water. Bedford, N. Y. April 27, 1929.



Fig. 179. Meadow mice, one to two days old, in their opened nest. Bedford, N. Y.

gray fox taken at Milford, Conn., he found rabbit hair, parts of a field mouse, sweet corn, pieces of apple, remains of a woodcock, and some leaves."

Seton ('25, pp. 491-495) likewise comes to the defense of the fox. From his own observations and the accounts of others he finds the red fox preying chiefly upon meadow mice, which certainly must be true in the more cultivated sections of our East. Two sample records from Seton are the account of the taking of a fox with seven mice in its mouth, and the analysis of four pellets composed of the fur of *Microtus pennsylvanicus* (90 per cent), a few mouse bones, one small feather, and the remnants of some apples.

COYOTE (*Canis latrans* and others). The coyote often depends upon mice for food. In Nevada at the time of the mouse plague, coyotes were frequently seen catching mice in the daytime, and their droppings were composed entirely of mouse fur and bones (Piper, '09b, p. 21).

Of 185 stomachs examined by licensed trappers and reported by Dixon ('25, p. 39), 47 contained rodents, presumably meadow mice among others. However, one-eighth of the rodents eaten were carrion and therefore of no significance in the question of rodent control.

DOGS (*Canis familiaris*). Farm dogs following the plow account for many meadow mice; and, it is said, sometimes learn to hunt independently when they acquire a taste for these mice. In irrigated districts many farmers keep dogs which they use to catch mice. They are particularly effective when the fields are being flooded, and the mice take refuge on the banks of the ditches (Piper, '09b, pp. 18-20).

BOB-CAT and LYNX (*Lynx rufus* and *L. canadensis*). The bob-cat and the lynx, though doubtless preferring larger game when available, habitually feed on meadow mice. However, being uncommon in cultivated districts, these cats can not be credited with an important economic status in such territory. Red-backed mice and lemmings must constitute at times a large proportion of their diet in northern territory. It has been shown by Dixon ('25, pp. 36-38) that the wild cats of California live largely on rodents. Out of 186 stomachs examined by trappers, 126 contained rodents. Dixon's laboratory examination of 32 stomachs showed that 44.5 per cent of their contents consisted of "harmful" mammals, 20.5 per cent of "beneficial" mammals, and 27.1 per cent of vegetation, soil, and parasitic worms.

HOUSE CAT (*Felis domestica*). The cats kept about dwellings for the purpose of holding in check the mouse populations, are rarely as efficient as they are frequently believed to be. Being well fed by

their owners, they but rarely have to forage for a living, and mouse hunting is only an occasional diversion. Most commonly they are kept for use against house mice, but in gardens and orchards near farm buildings they will at times hunt and take the voles as well. I have had described to me a daily exodus of large numbers of cats from a small Long Island community to hunt in a nearby marsh. Under such circumstances house cats possibly have some effect in holding down the field mouse population.

House cats have this drawback, that, unlike some of the wild enemies of meadow mice, they neither exclusively nor chiefly confine their attentions to mice. They are probably as efficient in the destruction of small game animals and song birds as in the killing of mice. It is consequently generally agreed that the world would be better off with a decreased house cat population.

No one has credited these felines with exerting an influence over the course of mouse outbreaks. Cats introduced in large numbers by orchardists in Washington were not alone capable of preventing an outbreak of *Microtus* in 1922-1923 (Couch, '28, p. 73), though as many as ten or twelve cats would not uncommonly be seen on three or four acres.

Since cats are known to be capable of transmitting such diseases as ringworm, tuberculosis, diphtheria, scarlet fever, and smallpox, there is good reason to be content with just a few about one's premises.

GRAZING STOCK. Of the domestic animals there are several that do more, though incidentally, towards keeping down the damage from meadow mice than do cats or dogs. Horses, cattle, hogs, sheep and goats, while—with the exception of the hogs—not eating the mice, so trample and destroy the cover where close grazing occurs that the possibility of mice long surviving is small. In the greatest strongholds of the meadow mice—that is, the swamps and marshes—such close grazing does not, of course, so frequently take place.

Agencies other than vertebrate animals that keep mice in check are as follows:

Parasites. In common with other mammals, the meadow mice have their full share of parasites, internal and external. The incidence of infestation is, of course, probably higher in years of overpopulation and crowding. Then these parasites might be expected to aid in the abatement of the plague, possibly through spreading disease. Such an influence, however, has yet to be demonstrated. Regnier and Pussard ('26a, pp. 449-450) record the following forms from *Microtus arvalis*. Ectoparasites: *Ctenophthalmus assimilis*

Tasch.; *Leptopsylla musculi* Dug.; *Ctenocephalus uncinata* Bak.; Haematopinidae; Sarcoptidae; Trombidiidae. Endoparasites: Spirochetes; Flagellata; Sporozoa; Haemosporidea; tapeworms; Trichurines; Oxyurines; Strongyloides; and Trichostrongilides.

The larvae of the botfly ("warbles") are said to be common in the voles in the vicinity of Touchwood Hills, Saskatchewan, writes Seton ('09, p. 531), quoting Edwin Hollis.

Disease. The Danyz virus, successfully used against *Microtus arvalis*. Europe's equivalent of our meadow mouse, in its times of over-abundance, is not known to occur naturally in our native mice. In the Buena Vista outbreak, however, the mice were seen to be sick and dying with some disease.

Of two hundred individuals of *Microtus californicus* taken from this area of mouse infestation, more than half died during the first month of captivity. Most of these showed symptoms of an infection which caused them to snuffle, and their eyes to secrete a yellowish serous fluid (Selle, '28, p. 94). F. E. Garlough and W. P. Taylor, in the field to investigate the outbreak for the U. S. Biological Survey, sent some of the sick mice to Dr. N. E. Wayson, of the U. S. Public Health Service. Doctor Wayson's report ('27, pp. 1489-1492) was as follows:

"They observed many sick mice of each of the two species [house mouse and meadow mouse]. The sick animals sat about with roached backs, roughened pelage, labored breathing, and with their eyelids glued together with purulent exudate, and were easily caught by hand. Carcasses which were partially destroyed, apparently by the cannibalistic feeding of the hordes of live mice, were also found. . . . Forty-two meadow mice and twelve house mice were submitted for examination, among these, 24 of the meadow mice and 6 of the house mice presented the gross pathology of a septicemia with the composite of the following lesions; Purulent conjunctivitis; congestion of the subcutaneous vessels producing a deep reddish pink color in the subcutaneous tissues, with greatest intensity about the superficial lymph nodes; swelling, congestion and infiltration of the superficial lymph nodes, with an occasional area of necrosis appearing as a white granule in the parenchyma of the node; scattered patches of deep red color, some of which were infiltrated (pneumonia) in the lungs, with a small amount of pleural effusion; enlargement of the spleen to two or more times its normal size, with congestion, and an occasional minute whitish area of necrosis; congestion of the liver with whitish dots of necrosis similar to those of the spleen; scattered subserous petechiae in the intestine.

“ . . . The organism was pathogenic to white mice and white rats, slightly pathogenic to a rabbit, and not pathogenic to guinea pigs. . . . Each of 10 white mice and 4 white rats was inoculated subcutaneously with from 0.3 cubic centimeter to 0.001 cubic centimeter of a 48 hour bouillon culture. All of these animals died in from three to five days after inoculation, with symptoms and lesions characteristic of those observed in the wild rodents. Two of three white mice, fed with bread cubes well moistened with the bouillon cultures, died with symptoms and findings similar to those found in the animals subcutaneously inoculated. . . .

“ . . . The symptoms and lesions observed in the wild mice, together with the reactions in the inoculated laboratory animals, and with the consistent bacteriological findings of a slender bacillus, appearing singly, in groups, and in thread forms, Gram positive, nonmotile, nonliquefying, non-gas-forming, facultatively aerobic and anaerobic, which grew in the gelatine stab in so characteristic a manner, seems adequate to establish the infection as that of *Bacillus murisepticus* or *Bacillus rhusiopathiae suis*. . . .

“ . . . Preisz and numerous others have determined it to be the cause of outbreaks of erysipelas, arthritis, and septicemia in hogs, in Europe, with large numbers of fatalities and great economic losses.

“G. T. Creech investigated its prevalence in the United States and determined that it was the etiologic factor in the ‘diamond skin disease of swine’, which he describes as a chronic form of swine erysipelas, widespread in the United States.

“J. V. Klauder has reviewed the subject of swine erysipelas in the United States, and its relation to erysipeloid diseases in man. He cites, and apparently accepts, the opinion of German investigators who have attributed these human infections to accidental inoculations from the tissues of animals affected with swine erysipelas. Such infections of man occur most frequently among those involved in animal husbandry, or in the slaughtering of hogs, and in the processing of their tissues for food purposes.”

From these findings it is apparent that there is some danger to swine and to humans from meadow mouse diseases in mouse plagues. Caution would be advisable under similar circumstances in any future outbreak.

The Annual Burning of Meadows. It is customary in many places, among them the New York City region, annually to burn over fields and meadows grown to long grass (locally called “fog”).

This burning usually takes place in the early spring, though fires are also set in autumn and winter. Spring is usually chosen since at that time there is less risk of the fire getting beyond control, and there is then more dead grass than green.

The reason for the burning of the grass lands in Westchester County, New York, usually is to reduce the danger to property from uncontrolled grass fires. But here and in other places these fires are, however, also set in order to give the new grass a better start, and thus improve the pasturage. The important effect these fires have in reducing the mouse populations in these favorite *Microtus* habitats seems rarely to be appreciated.

Doubtless a large proportion of the mice escape direct burning when a marsh is set on fire, both by fleeing in advance of the flames, and by retreating to their burrows. There are few broods of helpless young at the time the fires are set, so no great number of such are destroyed. But probably many adult mice die in the flames, and others are suffocated or baked in their underground nests. The most serious damage done to the mice lies, however, in the destruction of their food and cover. It takes at least two months, often more, to restore the proper conditions for repopulation.

After the burning of a marsh, there is usually no cover remaining, (Fig. 164), and often systems of runways and burrows are then revealed (Fig. 170) which show the former presence of large colonies of mice not before suspected.

Kennicott ('57, p. 87) observes that "after the annual fires have burned the grass on the prairies, numerous nests of the *arvicolae* may be found on the ground, the inmates of which, unable to escape, have often been killed, furnishing a feast to the many Hawks, Owls, etc., which flock to these grand barbecues."

FOOD

Food of the Meadow Mouse. The food of the meadow mice consists chiefly of grasses and sedges. These rodents are, however, omnivorous and will eat almost anything from tree bark to the corpses of their own kind. In the following list are mentioned such items of plant and animal food as have been definitely identified as entering into the diet of *Microtus*.

Sensitive fern (*Onoclea sensibilis*). Consumed by mice in my enclosure.

MONOCOTYLEDONS. GRASSES, etc. Grasses in general are eaten, used in nest construction, and furnish protection to the mice by cover-

ing runways. They are consumed the year around: leaves, flowers and seeds. If water is available, the prairie vole (*M. ochrogaster*) will even accept dry grass (Dice, '22, p. 39). When the grass is over-cropped, their food and cover is gone, and enemies, winged and four-footed, make great inroads among the voles. The following species are listed on the basis of the authorities named or on my personal observations, as indicated:

Blue grass (*Poa pratensis*): Among the more important foods of the *Microtus* of Sloop Island, New York (Hatt, '28, p. 92). I have also found it utilized in my quadrats (see the following section of this paper). Low spear grass (*Poa annua*): Extensively eaten by the *Microtus* of Sloop Island (Hatt, loc. cit.). Indian grass (*Andropogon* sp.): Rhoads ('98, p. 574). Salt grass (*Spartina* sp.): (loc. cit.). Rye, oats, wheat and barley: Cut down when nearly ripe. Fully matured grain is also eaten (Lantz, '06, p. 369). Maize: (Lantz, loc. cit., and Kennicott, '57, p. 99). Sedges and rushes (*Scirpus* spp., *Carex* spp., *Juncus* spp.): *Scirpus* sp. was among the plants eaten in my quadrats. Leaves, stems and seeds are eaten (Lantz, '07, p. 13; Rhoads, '98, p. 574). Wild onion: Bulbs eaten (Lantz, '07, p. 13). Blue flag (*Iris versicolor*): Commonly eaten. I have found its leaves cut into two- and three-inch lengths and carried to feeding platforms, runways, and burrows. *Iris* sp.: Seeds eaten (Lantz, '07, p. 13). Cattail (*Typha latifolia*): Roots eaten (Lantz, '07, p. 13); leaves eaten at Bedford, New York (personal observations). Hyacinth, tulip (cultivated): Bulbs eaten (Lantz, '07, p. 13).

DICOTYLEDONS. Sheep sorrel (*Rumex Acetosella*): Eaten by meadow mice in my quadrat. Buckwheat: Cut down when nearly ripe (Lantz, '06, p. 369). Tall buttercup (*Ranunculus acris*): Eaten by meadow mice in my quadrat. Turnips (cultivated): (Lantz, '06, p. 369). Sedum (*Sedum purpureum*) and strawberry (*Fragaria virginiana*), eaten by mice in my quadrat; strawberry (cultivated), particularly subject to attack (Lantz, '07, p. 13). Red clover (*Trifolium pratense*), eaten by mice in my quadrat. Sweet clover, roots eaten (Lantz, '07, p. 13). Alfalfa (cultivated), the roots the principal food of *Microtus montanus* in the Humboldt Valley plague (Piper, '09b, p. 6). Alfalfa is said to be the favorite summer food of *M. ochrogaster* (Lantz, '06, p. 369). Yellow wood sorrel (*Oxalis corniculata*), eaten by the mice in my quadrat. Parsnips and carrots (cultivated, Lantz, '06, p. 369). Primrose (*Primula parryi*), seeds eaten (Lantz, '07, p. 13). Wild morning glory (*Convolvulus scipium*), roots eaten (Lantz, '07, p. 13). Potatoes (cultivated).

eaten during the Humboldt Valley outbreak (Piper, '09b, p. 5, and Bailey, '08, p. 11).

Mullein (*Verbascum Thapsus*): In September this formed the principal food supply of a restricted insular colony of *Microtus* (Hatt, '28, p. 92). The tall stems were cut down and into lengths of six to ten inches. At least occasionally the stems were not at first cut from the base, but at some higher point. The leaves were removed in part and eaten. Empty seed pods and flower heads of a few mullein were found in the burrows.

Goldenrod (*Solidago* spp.): Eaten by the mice of my quadrat; on Sloop Island, Lake Champlain, the basal leaves of the goldenrod eaten in late summer. Aster (*Aster* spp.): Eaten by the mice of my quadrat.

Compass plant (*Silphium laciniatum*): Kennicott ('57, p. 99) writes of *M. ochrogaster* eating the large fleshy roots of this plant at least in autumn. He adds: "The root of this interesting prairie plant is sometimes a foot in length, and an inch or two in diameter at the top. To obtain it, they had burrowed down alongside, quite to the bottom, eating out the entire soft parts. Though so much eaten, none of it was found in their burrows."

Roman wormwood (*Ambrosia artemisiifolia*): Eaten by the mice of my quadrat. Jerusalem artichoke (*Helianthus tuberosus*): Tuber eaten (Lantz, '07, p. 13). Yarrow (*Achillea Millefolium*) and thistle (*Cirsium* sp.), eaten by the mice of my quadrat.

WOODY PLANTS. Larch (Lantz, '18a, p. 6). Scotch pine (*Pinus sylvestris*), seedlings commonly girdled. Juniper (Lantz, '18a, p. 6).

Willows: (Lantz, '06, p. 370). In the Humboldt Valley outbreak, small willows were killed by meadow mice (Piper, '09b, p. 6). Of the Buena Vista plague Piper ('28, p. 549) writes: "Near the willow thickets the mice continued in abundance, and not only had girdled many of the trees, but gnawed the roots of some so that they fell. Other standing trees had been completely denuded of bark even to the tips. Numbers of meadow mice were observed feeding high up in these trees on several occasions, as late as February 4. Scars of former girdling just above the ground line, and of gnawings on the trunks and branches appear to have been inflicted at least two years ago, and also at another period some years earlier."

Quaking aspen (*Populus tremuloides*): A small specimen in one of my quadrats was felled, but little of the bark was eaten. Bailey ('26, p. 91) says that aspens are sometimes peeled and killed by meadow mice. Silver poplars: Killed by mice in Humboldt Valley plague (Piper, '09b, p. 6). Carolina poplar (*Populus deltoides*):

Small seedling in my quadrat was felled and the bark eaten. Cottonwood (Lantz, '06, p. 370). Lombardy poplar: Large trees girdled in the Humboldt Valley outbreak (Piper, '09b, p. 6). Hickory trees in a plantation were girdled (Lantz, '07, p. 27). Alder (Lantz, '06, p. 370). Beech (Lantz, '06, p. 370 and '18a, p. 6); Merriam ('86, p. 274) states that he has seen saplings more or less completely girdled to the height of four or five feet. Chestnut: Plantation trees injured (Lantz, '07, p. 27). Oak: Acorns in a plantation injured (loc. cit.). Cork elm (*Ulmus racemosa*): Five shoots in my quadrat were felled and completely barked. Osage Orange (Lantz, '06, p. 370). Greasewood: A famine food in the Nevada outbreak (Piper, '09b, p. 6). Barberry, sassafras and currant bush (Lantz, '06, p. 370). Pear tree (loc. cit., and Ballou, '09, p. 53). Apple: Commonly killed by *Microtus* (Lantz, '06, p. 370). Crabapple, mountain ash and raspberry bushes (loc. cit.). Blackberry: Three small plants in my quadrat completely eaten. Lantz ('06, p. 370) records reported injury to bushes. Rose bush (Lantz, '06, p. 370). Black cherry, Lantz (loc. cit., and '07, p. 27). Plum and peach (Lantz, '07, p. 25). Locust: Cultivated specimens killed at Biltmore, N. C. (Lantz, '07, p. 27). Sumac (Lantz, '06, p. 370): Even under the famine conditions on Sloop Island, Lake Champlain, I found but one out of many sumacs present girdled and killed by *Microtus*. Sugar maple (loc. cit.). Red maple (*Acer rubrum*): Four out of five shoots in my quadrat were felled, the bark largely consumed on all. Merriam ('86, p. 274) states that he has seen saplings more or less completely girdled to the height of four or five feet. Buckthorn and grape vines, injured (Lantz, '06, p. 370). Nelson ('18, p. 406) states that a California meadow mouse destroys large quantities of drying raisins, seeking the seeds they contain. Dogwood and blueberry (Lantz, '18a, p. 6). White ash (Lantz, '06, p. 370). Bush honeysuckle (*Diervilla Lonicera*) (Lantz, '18a, p. 6). Snowball (Lantz, '06, p. 370).

CARNIVOROUS HABITS. Meadow mice will eat in small quantities almost any meat offered them. In their natural diet we find snails, crayfish (Lantz, '07, p. 13), larch sawfly cocoons (*Lygaeonematus erichsonii*) (Graham, '28, p. 301), and members of their own species (Kennicott, '57, p. 101; Bailey, '24, p. 525, and others). In captivity females sometimes devour their own litters, and adult males will eat the new born young that have the ill fortune to be quartered with them.

It is well known to everyone who has trapped *Microtus* that they are particularly cannibalistic, and that trap lines have to be gone over



Fig. 180. Quadrats A and B, shortly after completion. Bedford, N. Y.
June 21, 1927.



Fig. 181. Quadrat B in foreground, Quadrat A in rear. August 7, 1927.



Fig. 182. Like the work of a diminutive beaver; young cork elms felled by meadow mice in Quadrat B. August 7, 1927.



Fig. 183. The result of crowding. Small trees cut down in Quadrat B. August 7, 1927.

frequently if undamaged specimens are to be secured. In one marsh in which I trapped, in the first two days' collecting no trapped specimens were damaged by *Microtus*, but in the several days ensuing very few escaped such damage. Trapped *Microtus*, though gnawed about the body generally, were damaged particularly about the head. Trapped jumping-mice of the genus *Zapus* were, on the other hand, gnawed only around the base of the tail, as though the large glands in that region influenced the selection.

AMOUNT OF FOOD CONSUMED BY MEADOW MICE. Bailey ('24, p. 532) summarizes his observations and deductions on the amount of food required by meadow mice thus: "In one cage, 30 days' feeding of 10 mice with all the clover, cantaloupe, grain and seeds they would eat showed, after deducting 10 per cent for waste which could not be otherwise accounted for, that an average of 55 per cent of the weight of each animal was eaten every 24 hours. This was on the richest kind of food, such as they rarely obtain in the wild state.

"In another cage during the same period, nine that were fed grass, clover, and cantaloupe rinds, with no grain or seeds, ate, after deducting 10 per cent for waste, an average of 107 per cent of their weight every 24 hours. This would seem more nearly their normal ration in a wild state, and the best basis for computing food consumption. Some days they ate nearly twice their weight in green food, but only after they had become unusually ravenous. In both cages they had revolving wheels on which they exercised vigorously and were living fairly normal, contented lives.

". . . At 30 gm. a day one meadow mouse would consume 10,950 gm. (23 pounds) of green food in a year, and 100 mice 2,300 pounds, or a little over a ton of green grass or clover, which would make about half a ton of dry hay.

"A hundred mice to an acre is not an unusual number in meadows favorable to their habits, while in 'mouse years,' or during mouse plagues, the number has been estimated at thousands to the acre. Even with 1,000 to the acre it is easily shown that mice consume more vegetation (11½ tons) than would ordinarily grow on an acre in a year."

There are no data on the quantitative food requirements of any of the other voles considered in this paper.

Food of the Pine Mouse. "The pine mouse," according to Quick and Butler ('85, p. 116), "in winter lives upon the tender roots of young hickories, the young sprouts of the white clover (*Trifolium repens*), the fruit of the red haw (*Crataegus coccinea* L.) and the

tuberous roots of the wild violet (*Viola cucullata* Ait.). The first of these he uses for luncheon while excavating his runways. It is never found stored in his burrows, but as his passages approach these roots they expand, laying bare a large portion of the root from which the bark is generally entirely removed. The other products we find buried, the latter in numerous deposits, some of which contain a gallon of tubers and extend eighteen inches below the surface of the ground. This latter article evidently forms the bulk of their winter food."

Kennicott ('57, p. 103) writes that "By following these paths, I have observed where the meadow mice [pine mice] fed upon the roots of grass and various other plants, often digging down several inches for them; and I have in several instances found the bark gnawed from the roots of briars, etc. Hickory-nuts, hazel-nuts, and acorns were also found partly eaten in their tracks. The acorns of the burr-oak, and white-oak formed most of the stores collected in such burrows as I have examined."

Rhoads ('03, p. 102) was greatly impressed by the damage done to his garden in Camden County, New Jersey. Here the pine mice were excessively abundant: "In this garden not a meadow mouse cares to set foot in summer, yet these cousins of his destroy at least 20 per cent of the seeds planted, and 10 to 15 per cent of the growing and perfected potatoes, beets, parsnips, celery, cabbages and ruta бага turnips. They destroyed a whole planting of lima beans after growing in some cases to the height of eight inches, many replanted hills being eaten off three times. In the orchard, where meadow mice could not exist, these burrowing rascals have completely denuded the entire basal system of roots where they diverge underground from the parent trunk, in this way killing in 2 years apple trees 15 and 20 years old."

The injury which they do to agriculture, horticulture and silviculture is not always attributed to the proper agent. Often it is not discovered until later when leaves wither or an expected crop is found to have been devoured. Frequently the injury is attributed to the moles, which may on occasion use the same runways. The mole, however, is strictly a flesh eater, and when his course goes through a garden he is but in search of worms, grubs and digging insects which often are harmful to the crop in question. Shrews, too, are often likewise accused, with equal injustice, of damage they never do.

Food of the Red-backed Mouse. Rhoads ('03, pp. 93-94) writes of *Clethrionomys* thus: "He lives on the leaves and tender

stems of many weeds and grasses, and also enjoys the nuts and seeds of several species of trees, especially beechnuts, chestnuts, hazelnuts, and acorns, for which it frequently makes excursions into the dry upland forests and hill tops. It also seems to be fond of certain shelled snails, as *Omphalina* and smaller *Polygyra*, these being found in the retreats where the mice are trapped. They secure the snail by gnawing a hole into the apex of the shell, and drawing the body out backward. In winter I have found that they live almost entirely on the leaves of the evergreen strawberry bush, *Eryonymus americanus*, which grows abundantly in the cedar swamps and damp hemlock forests."

In his "Mammals of the Adirondacks," Merriam ('86, p. 271) remarks regarding this microtine: "It feeds upon beechnuts and a variety of seeds, berries, and roots, and also, at certain times in the winter season, upon the bark of shrubs and trees. The beech, maple, ash, and bass suffer most severely from its attacks, and in the order named. The bark is generally removed in irregular areas from the large roots just above the ground; but sometimes saplings, and even trees a foot (305 mm.) or more in diameter are completely girdled to the height of three or four feet (approximately 915 to 1220 mm.). The damage thus done to our deciduous groves is sometimes great, but does not compare with the ravages committed by the field mouse."

Two males caged with a female at the time of parturition attempted to eat her litter of new born young, and partially succeeded. Bailey ('26, p. 89) declares that these mice live chiefly on green food, but that bark and meat, too, are taken.

Food of the Lemming Vole. Relatively little is known about the food habits of this species. The following items are listed on the authority of Burt ('28, pp. 214-215) and Howell ('27).

Fungus (*Endogone* sp.): Mycelial threads and spores found in its stomach; blue grass (*Poa pratensis*)—leaves, stem, seed, the principle food. Lettuce (*Lactuca sativa*) and sweet potato, in captivity; and apple (*Pyrus Malus*), as trap bait. Beetle (Halipidae) fragments in stomach (Burt). Sedge (*Cyperacae*), leaves from stomach (Howell, p. 2).

Cabbage (*Brassica oleracea*) and green alfalfa (*Medicago sativa*) were refused, in captivity (Burt, '28, p. 215).

Burt (loc. cit.) concludes as follows: "The food of *Synaptomys* studied by the author was, in each case, chiefly blue grass, and consequently their excreta were green, whereas in all specimens of *Microtus* examined the excreta were brown or black. As was stated previously, the two forms are often found in the same associations.

However, in eastern Kansas at least, it is usually necessary to examine a runway for only a short distance to determine the form occupying it. If large, plump, brown or black excreta are scattered along the runway, it is possibly occupied by *Microtus*, but if the excreta are smaller, more slender and green, and distributed in small piles, one can be almost certain that the runways are those of *Synaptomys*."

QUADRAT STUDIES

To demonstrate the effect of a definite number of mice in a small area of uncultivated land, two contiguous quadrats were enclosed with a mouse-proof fence.

The method of studying the effect of rodent feeding by the utilization of quadrats has been successfully employed in the case of the Columbian ground squirrel (*Citellus columbianus*) (Shaw, '20, pp. 1-19), the kangaroo rat (*Dipodomys spectabilis*) (Vorhies and Taylor, '22, p. 3), the prairie dog (*Cynomys gunnisoni zuniensis*) (Taylor and Loftfield, '24, pp. 1-14), and in a restricted way with *Microtus* (Graham, '28, pp. 301-310).

My quadrats were established in the town of Bedford, Westchester County, New York. The site chosen was a low field in which *Microtus* normally occurs in small numbers (Fig. 180). The land was not pastured and the herbaceous growth in consequence was luxuriant. It was predominantly an open grass area, grown extensively with blackberries. Red cedars were encroaching upon the habitat, as is commonly the case on reverted farm land in this region. Other trees within a small radius were red maple (common), wild apple (common), white birch (few) and quaking aspen (few).

The ground cover was dominantly of grasses (*Poa pratensis* and others), *Sedum purpureum*, a yellow-flowered bramble, strawberry, yarrow, goldenrod, sheep sorrel, *Krigia amplexicaulis*, and daisies.

The habitat was bordered on the south by a stone wall, on the opposite side of which was an open hillside pasture. To the west it was limited by a young hardwood stand which covered the base of a hill slope. On the north side was a dry grass field, inhabited by *Microtus* in the wettest seasons only. On the east side was a hardwood swamp (Fig. 162).

Requirements Met in Construction of the Quadrats. The primary requisite of the quadrats was to keep mice within one of them, and exclude them from the other. In work on such a small scale it was further desirable to keep predatory vertebrates out of the two quadrats, but to allow free access to such invertebrates as

insects, which are normally present within the area. There should be no interference with normal drainage and the area should have full benefit of normal light, wind and precipitation. The quadrats as constructed met these requirements, with the exception that a small maple sapling which was cut, and fell across the barrier, permitted three mice to escape. There was no positive evidence that any predators ever entered the enclosures, the mere presence of the fence probably serving to keep such visitors away. Had it not been for trees and tall annuals within the quadrats, a screen could have been placed over them and additional protection given.

Specifications. The area enclosed measured 20 by 15 feet. A partition through the center divided this into two quadrats, A and B, each 10 by 15 feet, which were closely similar as to vegetation. Quadrat A was to be mouse free.

Posts of finished pine 2 x 2 x 24 inches, were spaced at five foot intervals along the line of the fence. These were driven thirteen inches into the ground. A trench eight inches deep and eight inches wide was constructed along the line of these posts. Galvanized fly-screening was then nailed to the posts so that it projected slightly over eight inches above the ground, eight inches vertically below the ground level, and had an overturn of eight inches horizontally, underground. To the upper margin of this screening was sewed (see Fig. 184) a twelve-inch strip of galvanized iron which received additional support by being firmly nailed to the three upper inches of the post tops.

There was thus presented to the mice a barrier of a twenty-inch wall, the lower eight inches of which were of screening and the upper twelve of a metal too smooth to climb and too high to jump over. Below the ground was a barrier of screening which, though small, was effective because of the shallowness of microtine burrows in such localities. The season's work proved this fence an effectual barrier over the top of which no mice were able to escape (except as above indicated), and under which no mice did escape.

Since quadrat B was designed to retain mice within it, and A to exclude them, they differed in two respects. Quadrat A had the supporting posts driven on the inside of the fence where they would aid an animal in escaping, and the underground horizontal screening directed outward, where it would interfere with burrowing operations of rodents on the outside seeking to get in, but would not interfere with digging of mice which had accidentally gotten in and were trying to escape. Quadrat B (Fig. 181) on the other hand,

had its fenceposts on the outside so that they gave no aid to a climbing mouse within the quadrat. The underturned screening here was directed inwards to prevent mice digging near the border from escaping in this way.

PLANTS: Quadrat B (occupied quadrat), June 27, 1927 (Figs. 180, 181, 185): Red maples (*Acer rubrum*), three small saplings, the tallest 7 feet; cork elm (*Ulmus racemosa*), one small clump 3 feet high; quaking aspen (*Populus tremuloides*), one sapling 3 feet high; yellow wood sorrel (*Oxalis corniculata*), abundant; roman wormwood (*Ambrosia artemisiifolia*), abundant; blue grass (*Poa pratensis*), abundant; sedge (*Scirpus* sp.), common; goldenrod (*Solidago* spp.), 1 species common; common sedum (*Sedum purpureum*), several; tall buttercup (*Ranunculus acris*), few; red clover (*Trifolium pratense*), few; asters (not yet in blossom), several; blackberry (*Eubatus* sp.), three plants; carolina poplar (*Populus deltoides*), one small plant.

On August 7, 1927, the following additional species were found: Thistle (*Cirsium* sp.), two plants; strawberry (*Fragaria virginiana*), few; sheep sorrel (*Rumex Acetosella*), one small plant; sensitive fern (*Onoclea sensibilis*), one present; yarrow (*Achillea Millefolium*), few small plants.

Quadrat A (mouse free quadrat), June 27, 1927. Like Quadrat B, except that none of the trees there listed were present and in addition there were the following: Wild apple tree (*Pyrus* sp.), one 3-foot sapling; strawberry (*Fragaria virginiana*); loosestrife (*Lysimachia quadrifolia*), few; common plantain (*Plantago major*), few; yarrow (*Achillea Millefolium*), few; timothy (*Phleum pratense*), few; rose (*Rosa carolina*), few, very small; black-eyed susan (*Rudbeckia hirta*), one plant.

HISTORY: April 18, 1927. The quadrats were both completed and were free of mice.

June 27, 1927. An inventory was taken of the flora of the quadrats.

June 29, 1927. Three *Microtus pennsylvanicus* were liberated in Quadrat B. These were: 1 adult female, 1 immature female and 1 juvenile male.

August 7, 1927. Since the quadrat was last visited, on June 29, 1927, the three mice had escaped, probably by way of a maple shoot which they felled (as previously mentioned) across the fence. Quadrat A presented a vegetation apparently more luxuriant than that in the field outside the enclosures, while quadrat B was almost completely denuded (Fig. 185). The young trees, except for the two



Fig. 184. Detail of Quadrat fence to show the method of joining the sheet iron to the screening.



Fig. 185. Red maple trees in Quadrat B, cut down and barked by meadow mice. August 7, 1927.



Fig. 186. The result of a small scale plague. Quadrat B. April 8, 1928.



Fig. 187. The summer after the mouse damage. Quadrat B. Contrast the area of Quadrat A in the background. June 10, 1928.

largest maples and four small elm shoots, were felled as though by a diminutive beaver (Figs. 182, 183, 185). The maples and aspen, though felled, were but partly divested of their bark. The Carolina poplar had had its leaves eaten, but no bark was removed. The grass was thin and mostly dead. Many herbs had entirely disappeared (Table I). One above-ground nest, numerous runways, and one tunnel were observed.

September 5, 1927. An immature *Microtus* was liberated in quadrat B. There was no noticeable recovery from the damage described on August 7. The quadrat was flooded at this date, about one-half of it being under water an inch or less deep.

September 8, 1927. The mouse introduced on September 5 was still present and alive. Freshly cut grass was noticed. There was a newly constructed nest with a thin roof admitting light and rain.

September 10, 1927. Another *Microtus*, three-quarters grown, was liberated in quadrat B. The first mouse was still there and alive.

December 11, 1927. About half of quadrat B was covered with a thin sheet of water and ice. Snow and ice occurred also in other spots in the enclosure. The nest contained one dead and frozen mouse. It could not be determined whether this mouse had died as a result of exposure or of starvation. There was no trace of the other. This missing mouse, may of course, have been eaten by its companion, by some carnivore, or it might have escaped over a snow-drift formed during the heavy snowfall of December 4 and 5. The vegetation was almost completely gone, as indicated in Table I.

April 8, 1928. Quadrats visited and photographed (Fig. 186). The spring growth had not yet started. The fences were removed.

June 10, 1928. Quadrats visited and photographed. The area of quadrat B still had but scant vegetation (Fig. 187). *Sedum* alone of all the plants represented the previous year was equal in development to the growth in the surrounding area. It was here graphically shown how overfeeding by mice in one year affects the growth of the succeeding season.

The quadrats constructed failed to produce all the results which such a method makes possible, partly because of the lack of time properly distributed to devote to the problem. Having to construct the quadrats almost entirely alone, their size and their number were seriously curtailed. I was unable to find time to visit the quadrats regularly or to trap for living material to introduce into the quadrats. With a series of quadrats in different habitats, one could obtain comparable data of more value. Also, the mouse populations of such quadrats should either be kept constant or self-limited.

Observations should be made over a period of more than one year.

Table I. Showing status of the vegetation in quadrat B, 1927. On June 27, no mouse feeding had been done. August 7, three *Microtus* had fed for less than 5 weeks. December 11, two *Microtus* had feed for less than fourteen weeks.

<i>Name of plant</i>	<i>June 27</i>	<i>August 7</i>	<i>December 11</i>
Red maple	5 shoots, the tallest 7 ft.	3 smallest shoots felled	1 shoot standing. Denuded of bark for 2 feet
Cork elm	5 shoots	1 felled	All felled. Completely barked
Quaking aspen	1	1 felled	As August 7, not barked
Carolina poplar	1	1 felled	As August 7, barked
Blue grass	Abundant	About $\frac{3}{4}$ gone	Very thin cover remaining
Yellow wood sorrel	Abundant	None	None
Roman wormwood	Abundant	None	None
Sedge	Common	None	None
Goldenrod (2 spp.)	Common	None	None
Sedum	Several	None	None
Aster	Several	None	None
Red clover	Few	None	None
Tall buttercup	Few	None	None
Blackberry	3 plants	None	None
Thistle	None	Two	None
Strawberry	None	Few	None
Sheep sorrel	None	Few small plants	None
Yarrow	None	Few	None
Sensitive fern	None	One	None

EFFECT OF VOLE FEEDING ON FARMING

The charges of the farmers and their government agencies against the meadow mouse and the pine mouse are serious and repeated. Rarely has anyone had the courage to question the status of these claims.

Certain it is that mice do kill trees, destroy gardens, and eat vast quantities of cultivated crops. We have all seen such instances. The flood of complaints and appeals for aid that come in to federal, state and county agricultural bureaus are not founded on myth. The only questions which we may dare propose are:

1. Which species of mice are responsible for the injury?
2. To what extent are the conditions to be combated general and continuous and to what extent local and periodic or occasional?
3. Are there compensatory features in the existence of the mice that should be considered?

Let us examine first some of the charges made by farming interests against these mice, outside of definite plagues.

Damage to Field and Forage Crops. Quoting Lantz ('06, pp. 368-369): "In recent years the Department of Agriculture has frequently received complaints of damages to meadows and pastures by field mice. The common meadow mouse (*M. pennsylvanicus* and its various subspecies) is usually the offender in these cases, although the prairie meadow mouse (*M. ochrogaster*) also causes considerable loss in the West. Both these mice work under the snow in winter, burrowing along the tops of the succulent roots of clover and other plants, and sometimes destroy entire meadows, which have to be plowed up and resowed. Such damage usually occurs where a thick growth of grass is left in the field in fall. Closely mowed or closely pastured fields are not usually badly injured by mice.

"The destruction of corn and wheat in the shock by meadow mice is common, and growing crops—wheat, oats, barley, rye and buckwheat—are often cut down and eaten. The damage to standing grain is most noticeable when it is nearly ripe, but fully matured grain also is eaten. Short pieces of the stems of grains and of grasses scattered along the runways of the animals are conclusive evidence of the nature of their diet. In alfalfa and clover fields considerable loss is frequently caused by meadow mice. The ground is often littered with leaves cut from the plants. Stomach examinations of a dozen specimens of *Microtus ochrogaster* captured in alfalfa fields during the summer of 1905 showed that their diet was almost exclusively leaves of alfalfa. When field mice occur in normal numbers, the losses are not serious; but when local conditions have favored an abnormal increase of the animals, the loss of crops is enormous."

Bailey ('24; p. 533) writes: "Mouse plagues, disastrous as they are locally, are of minor importance in comparison with the steady yearly drain on crops by the mice over the country at large in normal years. Even as few as 10 meadow mice to the acre on 100 acres of meadow would take about 11 tons of grass, or 5½ tons of hay, a year. Or this number on the 65,000,000 acres of hay raised in the 38 mouse states would cause a loss of over 3,000,000 tons of hay a year, or a money loss of some \$30,000,000 annually in hay alone."

And Bell ('21, p. 431): "Stockmen were quick also to see that the saving of alfalfa and range grasses from being eaten and uprooted by rodents afforded an immediate means of carrying and finishing for market greater numbers of cattle and sheep, thus increasing the urgently needed supply of meat, hides, and wool. With the enthusiastic and hearty cooperation of extension directors, county agents, State officials, farmers and stockmen, the work has been extended until now it embraces thoroughly organized aggressive campaigns in 16 western States."

Damage to Fruit Crops. "The Biological Survey," says Lantz ('06, p. 370), "has received complaints of the destruction of apple, pear, peach, plum, quince, cherry and crab-apple trees; of blackberry, raspberry . . . [and] currant . . . bushes, and of grape vines." And further ('18a, p. 6), "Older orchard trees sometimes are killed by meadow mice: In Kansas in 1903, the writer saw hundreds of apple trees 8 to 10 years planted, and 4 to 6 inches in diameter, completely girdled by these pests . . ." And in the Arnold Arboretum, Boston, in the winter of 1903-4, "meadow mice destroyed thousands of trees and shrubs, including apple . . . [and] blueberry."

Nelson ('18, p. 406) writes that "One species in California destroys large quantities of raisins drying in the field by carrying them off to some shelter, where they cut out the seeds and leave the rest of the fruit. I have seen half a pound of raisins under a piece of board, the result of the night's work of a single mouse."

In order to make a strong impression as to the seriousness of rodent damage, authors whose chief interest is in control or extermination often give figures estimating—conservatively in most cases—the damage done over a large area. Thus in one report we read: "It certainly would not be far beyond the bounds of conservatism to figure the loss and injury at one dollar per acre per year, including all ages and conditions of the apple, pear, and plum orchards of the state . . . Thus do we find . . . there is probably incurred annually the astounding loss of over \$200,000 in [the state]." Now if this author had only taken the trouble to add the value of the crop from this same acreage, his estimated damage would have seemed an insignificant tax that the farmers could well afford to pay for the benefits derived. This is true of many figures one may find in such reports. It cannot be denied, however, that local conditions frequently are serious and without protective measures horticulturists would have to take frequent losses which they could ill afford. Thus \$10,000 damage was done to one farm by mice, and \$100,000 is the estimated injury to fruit and shade trees in a single county in a "mouse year." Damage to the amount of \$500,000 was estimated to have been done to the fruit trees in Connecticut at this time, certainly a heavy burden (Silver, '24b, p. 173).

Damage to Truck Crops. Lantz ('06, p. 369) writes: "The meadow mice are destructive to market gardens. Strawberry fields are especially liable to attack, because of the mulch used to protect the plants and because of the animal's fondness for the succulent

crowns of the plants themselves. These mice destroy seeds in the garden, hotbed, or cold-frame, potatoes in the ground, and many other growing vegetables. In the fall they destroy beets, turnips, carrots, parsnips, celery, apples, and potatoes, when piled on the ground or stored in pits." But he significantly adds: "The depredations may to a great extent be prevented by the careful burning of weeds and other trash which harbor the pests."

Damage to Forest and Ornamental Trees and Shrubs. In this connection Lantz remarks (op. cit., p. 370): "The Biological Survey has received complaints . . . of the injury of sugar maple, black locust, Osage orange, sassafras, pine, alder, white ash, mountain ash, oak, cottonwood, willow, wild cherry, and other forest trees." It is also written that rose and barberry bushes are destroyed.

Further (loc. cit.) it is recorded that "in the Arnold Arboretum, near Boston, Mass., during the winter of 1903-4, meadow mice destroyed thousands of trees and shrubs, including apple, maple, sumacs, barberry, buckthorn, dwarf cherry, snowball, bush honeysuckle, juniper, blueberry, dogwood, beech and larch. Plants in nursery beds and acorns and cuttings in boxes were especial objects of attack." And (Lantz, '07, p. 27) "Dr. C. A. Schenck, forester of the Vanderbilt estate, Biltmore, N. C., in a recent communication to the Biological Survey, states that plantations of locust and black cherry suffer badly from the girdling of mice, 'especially the locust, which are killed outright, usually the best specimens.' And, he adds, 'Plantations of acorns, chestnuts, and hickory nuts are rendered impossible because of the ravages of mice.'"

Microtine Damage to Scotch Pine. Damage to one plantation of Scotch pine in the Harvard Forest and one near North Ashburnham, Massachusetts, is characteristically microtine. The habitats bordering the damaged plantation in the Harvard Forest are more favorable to *Clethrionomys* than to *Microtus*. It is the writer's belief that the first form did the girdling.

The Harvard plantation showed complete girdling of practically all trees that were injured. It would appear that the mice conserved energy in removing the outer bark by feeding on one tree until all within reach had been utilized. At North Ashburnham girdling was complete in only about twenty-five per cent of the cases. The denuded belt extended from the ground to a height of six to twelve inches. Inward, it continued through the cambium (Figs. 210-212).

The individual tree is damaged in ratio to the amount of girdling. An incompletely girdled tree does not die, for a swelling is produced

in the side opposite the injury by means of which the food and water supply to the part above are maintained. However, since the bark does not regenerate over the place of injury, the tree is destined to die before maturity, provided the injury extends over more than one-half the circumference of the tree. This is because of the resulting weakness of the base. The immediate effect produced is a marked stunting of growth, most severe the first season following injury and increasingly less in subsequent seasons. If girdling is complete the tree usually dies within a few months. In a small percentage of the cases, however, the tree forms a huge swelling above the denuded ring and the transpiration stream is apparently reestablished in the deeper-lying layers. Such trees do poorly and in most cases die within three years, though a few in the Harvard Forest were still alive eight years after the injury. These trees appeared then to be very near death. The weakened non-growing tree base eventually will cause their destruction, even though physiologically the trees are able to maintain life. A few other trees that have been girdled slightly above the base have diverted all their growth energy into one of the laterals below the band of girdling. This lateral then turns upward at a right angle and parallels the old dead trunk (Fig. 211). The tree thus making a last abortive attempt to live, even though it is able to establish itself firmly enough by roots to support the new trunk, has lost as many years competitive growth as its age represented when the mice attacked it. Its one hope is in an already well established root system.

In the Harvard Forest plantation about 51 per cent of all the trees were girdled, and 21 per cent were killed from this cause. The North Ashburnham plantation was 59 per cent girdled. Of the girdled trees about one-half were yet alive. The trees in the first plantation were eight years old at the time of injury; in the second, about six years old.

In each plantation injury was local in distribution, adjacent trees being affected, rather than scattered trees throughout the stand. In one instance 83 adjacent trees were killed while approximately an equal number of dead ones were scattered among the living.

Two other Scotch pine plantations in the Harvard Forest, each about one mile from the one damaged, and of approximately the same age, showed no injury.

Injury to the trees of the Harvard Forest was done in the winter of 1917-18, though there are no records as to the months or the period of duration. The owners of the North Ashburnham planta-

tion stated that the injury there was accomplished about 1916. It is probable that the voles, in the years of attack on Scotch pine were in a period of over-population and that crowding caused them to use food sources not ordinarily utilized. The fact that mouse damage was not repeated each winter has given the plantation some chance of continued growth. The mice girdled the Harvard Forest trees during a period of heavy snowfall, and, judging from the level of the injury, worked from tunnels in the snow.

Mouse girdling of Scotch pine is apparently not uncommon in the eastern United States. The writer has observed similar injury near Katonah, New York, and Greenwich, Connecticut. Silver ('24a, p. 5) cites a case in New York of the complete girdling of one thousand six-year-old Scotch pines in a five-acre block. This he attributed to *Microtus*. Plantations which I have examined at South Mountain Park, New Jersey, Millbrook and Saranac Lake, New York, showed no injury.

A cursory examination of a number of conifer plantations bordering reservoirs of the New York City water supply, located in Westchester County, has shown the necessity of clearing out the ground cover in these plantations. In many plantations, typified by one near Katonah station, the trees have been cleared of their lower branches, and the ground below of grass. There being no suitable cover, there were no mice and, in consequence, there had been no damage.

The other condition was fairly represented in a 10-acre mixed plantation of red or Norway pine, Scotch pine and white pine, on the border of Cross River reservoir. There the undercover, in 1927, had not been removed. Grass, briars, and many herbs formed a rank and deep habitation for a large colony of mice and rabbits. In the area of Scotch pine, there was a large section of microtine girdling. Of the trees injured, only about twenty were dead; and partly girdled trees were stunted. Whether meadow mice or pine mice were responsible for this injury could not be told, since the bark had been removed above ground, and this might have been done by either species working under the snow. None of the other conifers in the plantation showed injury.

It would seem essential in this district to keep the ground clear in the plantations of Scotch pine until the trees have reached a basal diameter of eight or ten inches, after which they seem to be immune to attack by the mice.

GOOD SERVICES OF VOLES

It is an ill wind that blows no one any good, and an unknown animal that is a useless pest. The voles till the soil, particularly in easily worked wet lowlands, where their burrowing activities are conducive to better drainage and an increased growth of vegetation. They supplement the work of the earthworms, e. g., in bringing the subsoil to the surface and in carrying vegetable matter into underground burrows. Rains and floods wash more decayed vegetation into these tunnels while the excreta and dead bodies of the mice all help to enrich the soil, in a way that is not spectacular, but, perhaps, if considered in periods of decades and centuries will be recognized as of the greatest importance. They are, in the areas which they occupy, unrivaled in their roles of converting waste vegetation into flesh for three quarters of our carnivorous birds of prey, predacious mammals and reptiles. With the extermination of these mice there might appear a hoard of voracious mouths developing new food habits, which might inconvenience the farmer more than do the mice. The fur crop of the microtine area, too, is controlled in large part, though indirectly, by these mice. Where winter trapping of fur bearers is done, it is probable that the mice indirectly turn more money into the farm than they take from it, while those fur bearers which hunt the mice perform of course the important task of policing the surplus mouse population. There must be a point of balance between populations of rodents and their enemies at which each functions most efficiently. With over-population of the grass eaters, it means an under-population of the flesh eaters, and the latter can no longer control the former. Over-reduction of the carnivores naturally produces this mal-adjustment. On the other hand, given too few mice, their hunting becomes unprofitable to the carnivores, which must then turn their attention to other food, move to other districts, or starve. The vestige of the rodent population, then unharrassed by their natural pursuers, is likely to stage a comeback to their former numbers. If the mice were entirely exterminated, others of our now useful animals would probably be transformed into pests in the eyes of agricultural interests.

If one insists on some more tangible value than this, Graham ('28, pp. 301-310) has pointed it out. The larch, one of our important forest trees, flourished with few enemies until about twenty years ago, when the larch sawfly appeared in great numbers. This hoard sped rapidly through the larch areas and killed approximately 60 per

cent of these trees in the Lake States, an almost incredible amount of timber. Enemies of invading pests do not often appear quickly enough to check the destructive spread, but when we find an animal which will prey upon the invading hosts, then it should be wisely encouraged. Graham found that the meadow mice were killing a large number of the prepupae of these sawflies. Of the extent of this destruction he writes:

"Cocoons were placed . . . on 12 sample plots on August 24, 1927. On November 4th of the same year a preliminary examination was made, the results of which . . . show clearly that the small mammals are in some cases very thorough in their search for cocoons. An average of all the plots showed a total destruction by November 4th of 55 per cent of the cocoons. Doubtless this work will continue throughout the greater part of the winter.

"On the different plots there was considerable variation, from 20 to 78 per cent, in the number of cocoons destroyed. This variation is interpreted to indicate that the abundance of the animals concerned varied in the same proportion."

A part of the ground had a cover of sphagnum and sedges. "On this plot none of the cocoons buried in the moss-sedge area were disturbed, whereas on the other part of the plot every cocoon was gone. From these observations it would appear that the comparative abundance of mice and other small mammals that feed upon the hibernating prepupae of the sawfly, may be measured by the effect of these animals upon a constant number of fresh cocoons distributed over a given area in a uniform manner.

"The larch sawfly, *Lygaconematus crichsonii*, is one of the very important defoliators of the northern swamp forest and during the past twenty years has reached epidemic proportions and killed an amount of tamarack timber almost too great to comprehend. The young trees that survived this outbreak are growing and reproducing well but the sawfly is a continual menace to this forest.

"Unless practical control measures can be developed it is almost certain that another such outbreak will occur in the future, and will then cause a much greater economic loss than the last outbreak because of the present increased value of tamarack timber.

"Inasmuch as direct methods are too expensive to use in the control of this insect in tamarack forests it is necessary that indirect or preventive methods be developed. . . .

"Of the biotic factors that tend to reduce the numbers of sawflies during the cocoon stage, insect parasites, entomophagous fungi, and certain small mammals are important. Of these the small mam-

mals are by far the most important. Parasitic insects and fungi kill less than 10 per cent of the prepupae, whereas mice and shrews destroy, on the average, from 50 to 80 per cent. Mice appear to be more important than shrews in this work.

"The effectiveness of mice in destroying the larch sawfly prepupae varies with the natural abundance of these animals. In those swamps or parts of swamps where the ground cover is made up of a great variety of woody and herbaceous plants, mouse food is abundant, and the mouse population is great. The destruction of sawflies is likewise great. On the other hand when the ground cover consists primarily of mosses and sedges, food for mice is comparatively scarce, and as a result the mouse population and the destruction of sawflies by them are correspondingly less."

When we point to the striking evidence of damage wrought by voles, let us not forget that they are in the main an asset if we do not blindly destroy the agencies that hold them within proper bounds in the natural way.

BREEDING

Pairing and Mating. MEADOW MOUSE. I can do no better than quote Bailey ('24, pp. 526-529) on the pairing and mating of meadow mice.

"The mating of a strange male and female often begins with several little fights in which the male sometimes gets a bloody nose, while the female seems never to be injured, but usually after a few minutes they are fully mated and the affair has passed as a mere formality of microtine etiquette. If the female is not ready for mating she may keep up attacks on the male until he is forced to retire to a corner and nurse his injured feelings, if not an injured nose. . . . 'Mating' is only for the immediate needs, and a misnomer at that, because a female usually accepts the attention of any number of males in rapid succession and shows no choice of individuals, favor to young or old, or any regard to relationship, whether sire or brothers or previous offspring. There seems to be no moral necessity of life with them other than the most rapid increase possible of individuals of the species. The one exception to a complete promiscuity is provided by nature in the slower sexual development of the males, which prevents inbreeding within the litter before the young have scattered, the males not coming to sexual maturity until about the time the first young of the females of the same litter are born. Furthermore, respect for the females during pregnancy by

even the most virile old males is enforced with such spirit that it seems never to be questioned.

"Certain pairs will live together in perfect accord, while others will quarrel and fight and refuse to occupy the same nest. Some females will accept the attentions of only one male and will savagely resent the advances of all others, while others show no preference and will accept attentions promiscuously.

"Most of the males are highly polygamous, but one pair that lived together until after the young were born were from the first very affectionate, remaining much of the time together in the nest box, and paying little attention to the mice in neighboring cages. This male would not voluntarily leave his cage nor enter the cage of another female, even when called. This was very unusual, as most of the males were eager to go into other cages and make friends with females or fight with the males.

"In No. 6 cage, a male and female had lived contentedly together and raised two families of young while against their cage an old female lived alone in No. 3, and was on friendly terms with her neighbors through the wires. After she had given birth to her fourth family of eight young, she was making her peculiar squeaking calls, which the male in the other cage evidently recognized as an invitation to visit her, and as he eagerly came up over the edge of his cage and down into hers the female in cage No. 6 became greatly excited and twice forced her way out under the roof of her cage and tried to get into cage No. 3 to punish her rival. Not being allowed to do this she stormed around her own cage, squeaking, kicking up the sand on the floor, biting the wires, and showing every indication of rage until her mate came home in the evening. Then she pounced upon him, bit his nose, chased him around the cage, squeaking and scolding at him until he was severely punished. She was cross with him all the evening, but the next day had settled down to her usual pleasant frame of mind and had evidently forgotten her domestic troubles.

"A neighboring male that came into cage No. 1 during the mating time of the old pair that had been captured in their wild state was pounced upon by the female and his foot so badly bitten that he was glad to escape to his own cage and nurse his bloody paw. In other and the majority of cases the females made no objection to their mates visiting other females as much as they wished, and these two cases are exceptions to the usual free-love manner of life among these polygamous little animals.

"These incidents, however, show variable tendencies in the social life of the meadow mice, which, under certain conditions of the environment, might lead to perfect monogamy if for any reason this should prove beneficial to the species."

RED-BACKED MOUSE. Mating behavior of captive red-backed mice is at least on occasion a matter of the male forcibly overcoming the resistance of the female. In one such instance, among my captives, two males were pursuing one female for about twenty-four hours, at which time she gave birth to three young and was caged separately. During the pursuit by the suitors, however, she was successful in breaking a leg and blinding an eye of one of her followers, which incidentally, did not seem to diminish his fervor. A day after the birth of the young, all of which had been killed by the males within a few minutes of parturition, the female was caged with a single male—the one she had badly injured. After a few minutes of running fight, the male accomplished his purpose. Later they settled down to a more peaceful existence and shared a nest together.

Gestation. The eastern meadow mouse, according to Bailey ('24, p. 528), has a period of gestation of approximately 21 days, in one case 20 days and 17 hours.

In *Microtus californicus*, Selle ('28, p. 96) has found the period of gestation to be close to 21 days (22, 21, 21, and 20 days 12 hours). This is the time required for several other mice the period of gestation of which is known, and probably applies to the pine mouse, red-backed mouse and lemming vole.

Litter Size. **MEADOW MOUSE.** The average number of young produced in a litter varies with the species. In *Microtus pennsylvanicus*, according to Bailey ('24, p. 528), the female produced "litters of usually 4 at first, but when full grown, after the first or second litter, usually 6 or 8 at a birth . . . The number of young in a litter ranges from 2 to 9, and with the original pair, averaged 5, totaling 83 in 17 litters." I have taken specimens which contained from 4 to 6 embryos each.

In *Microtus arvalis*, of France, according to Regnier and Pussard ('26a, p. 418), the average litter is five or six, but as many as eleven may be born at one time.

Microtus uanous, a vole of the Rocky Mountains, has been known to bear 13 young (Lantz, '07, p. 11).

In *Microtus montanus yosemitae*, Grinnell and Storer ('24, p. 125), found the litters ranging from 4 to 9, with an average of 6.3 in 30 specimens.

In *Microtus mordax sierrae*, Grinnell and Storer (op. cit., p. 133) recorded 3 to 7 embryos per litter with an average close to 5 for 21 females.

The mammae in *Microtus pennsylvanicus* consist normally of two thoracic pairs, and two inguinal pairs. This would seem to limit the number of young that could be raised in one litter to eight.

In times of mouse "outbreaks" the litter size of many species is said to increase. This has not yet been established for meadow mice, but it should be a relatively easy matter to settle.

In a series of 148 stock female white rats, King ('24, p. 340) found that there was a steady decrease in number of young per litter after the ninth.

PINE MOUSE. Lantz ('18a, p. 7) states that these mice are less prolific than meadow mice. Rhoads ('03, p. 104) writes of a nest containing five young, three of which were twice as large as the other two, and hence possibly of another litter.

RED-BACKED MOUSE. A female at Petersham, Mass., gave birth to three young on July 4. Another, taken September 3, contained six embryos, five in the left uterine horn and one in the right. Merriam ('86, p. 272) records broods of four each. Dice ('25a, p. 24) notes two females with four embryos each. Bailey ('26, p. 89) found females carrying usually from 4 to 6 young, and occasionally 8. Dice (loc. cit.) states that the mammae are pectoral, 2 pairs, and inguinal, 2 pairs.

LEMMING VOLE. Burt ('28, p. 214) states that from one to seven young are brought forth in a litter, and that the number of embryos found at different seasons of the year indicates that the size of the litter is less in cold than in warm seasons. Linsdale ('27, p. 54) records uterine complements of four and five embryos; and gives variations of mammae from 4 pectoral and 2 inguinal (two specimens) to two pectoral and two inguinal (one specimen).

The Breeding Period. MEADOW MOUSE. "In captivity the young, if well fed, begin to breed when less than half grown, the females mating with older males when only 25 days old and having young when 45 days old, and the young males mating when only 45 days old. The period of gestation is approximately 21 days, in one case 20 days and 17 hours. The breeding activities are practically continuous, the females mating immediately after the birth of the young, and producing litters of usually 4 at first, but when full grown, after the first or second litter, usually 6 or 8 at a birth. Seventeen consecutive litters of young have been produced by one female in captivity within a year—May 25, June 14, July 8, July 29,

August 23, September 18, October 18, November 9, November 30, December 21, January 12, February 2, February 23, March 18, April 8, April 30, May 20 and then she showed no signs of being near the end of the breeding period, while several generations of her young have been busily following her example, one of them, born on May 25, having produced 13 families of young, totaling 78 in number, before she was a year old." (Bailey, '24, p. 528).

There is reason to believe that in Nature the breeding season is not so long nor quite so continuous. However, if conditions are favorable, it is possible for the population to increase at such a rate as that among Mr. Bailey's caged mice. Then it is that mouse plagues may break out. In trapping for *Microtus* I have found during the summer few adult females which did not contain embryos or evidence of recent parturition.

Selle ('28, p. 94) concluded from his extensive sampling in the Buena Vista mouse plague that breeding ceased about the last of October or the first part of November, for no young less than half-grown were found at the time of his visit.

RED-BACKED MOUSE. A female in my possession at Petersham, Mass., gave birth to young on July 4. At this place, too, I took a female on September 3, which contained embryos measuring three millimeters from crown to rump. Five of these were in the left uterine horn, one in the right. Merriam ('86, p. 272) writes of taking females containing young as early as April 3, and as late as October 4. He also states that in June he has taken a female that was nursing her second brood.

LEMMING VOLE. Pregnant females have been taken at every month in the year by Burt ('28, p. 214). Quick and Butler ('85, p. 114) found them breeding from February to December. Linsdale ('27, p. 54) records gravid uteri March 13 and December 8.

Development of the Young. MEADOW MOUSE. Again quoting Bailey (op. cit., p. 530): "The young are hairless and weigh only about 3 gm. each when born, with closed eyes and ears and no trace of teeth. They grow rapidly, however, gaining after the first few days about 1 gm. a day until over half grown. Their dark-colored fur begins to appear as soft velvet in five or six days, their incisor teeth about the fifth, the molar teeth about the seventh, and their eyes and ears open on or near the eighth day. As soon as their eyes are open they are quick to run and hide if disturbed, and a few days later are out of the nest searching for food, following the trails, and, if in cages, running on the wheels, playing and pushing for their rights.

"When about 12 days old, the young are weaned, but they remain with their mother, occupying the old nest and holding together in friendly family relations until time for the next installment of young, when the mother seeks or builds a new nest and leaves her previous family to care for itself. If food were abundant, they would remain contentedly together for an indefinite time but for the disturbing sexual forces which before they are full grown impel the females to seek new homes for prospective offspring and the males to wander constantly in search of one mate after another."

I took five young from a nest, September 11, 1927, and the following description of one will serve equally well for the others:

Total length, 56 mm; tail length, 10 mm; length of hind foot, 8 mm; height of ear from crown, 1 mm. Eyes not open. External auditory meatus not open. Skin fits loosely over the body. Upper lip neither free nor cleft. A fine pilosity over the whole body. Vibrissae well developed (an aid in nursing?). Incisors not erupted, but appear under the gums as bumps. The back, dorsum of all feet, and all of tail, a steel-blue gray, grading through lighter gray on the sides to a transparent pink beneath. A stump of the umbilical cord remains attached.

Movements of the young were feeble and apparently thigmotropic. When placed in water there were feeble and futile swimming movements of the legs; the surface tension seemed sufficient to retard their progress. These young were probably less than two days old.

Selle ('28, pp. 96-98) has described the young of *M. californicus*: Young at birth averaged in weight 2.7 grams, in a litter of June 17. A litter dropped August 1 averaged 3.66 grams. Their eyes usually opened on the ninth day, although in some they did not open completely until the tenth.

The young of this species nursed at least 23 days, when they averaged 27.1 grams in weight. They had, however, been accepting other food after about the ninth day.

The gain in weight of a litter of five, born June 17, is as follows:

Date	Age	Average weight (grams)
June 17	At birth	2.70
June 22	5 days	5.44
June 27	10 days	8.30
July 2	15 days	13.10
July 7	20 days	21.00
July 12	25 days	30.00
July 17	30 days	36.06
August 1	45 days	50.06

The average gain per day was 1.12 grams, for thirty days. At the end of this period their actual individual weights were, for the males, 41.90, 40.70, 36.00 grams; and for the females, 34.40 and 32.90 grams. Eighteen other records show a marked difference between the sexes in age weights of young and adults of this species, the females being lighter in each series.

As among other mammals, there may be marked variation in size among the young, even those of one litter. From one uterus I have removed embryos whose crown-to-rump lengths were respectively 29, 27, 27 and 23 millimeters.

RED-BACKED MOUSE. The young of a litter born July 4, at Petersham, Mass., measured 30 mm from crown to rump, and 39 mm from tip of nose to tip of tail. The tail was 6 mm long; and the hind foot 6 mm. These mice were blind, naked, and but loosely enveloped in their skin.

Care of Young. MEADOW MOUSE. Regarding the attention which meadow mice give their young, Bailey ('24, p. 529) writes:

"In cold weather the nest is built especially thick and warm, and the newly born young are not left for more than a few minutes at a time, and then the mother covers them up securely before she leaves them.

"One old mother in No. 3 cage had a new family one cold night in March. In the morning she was very hungry for her breakfast when it was placed in the cage, but was greatly worried about the young getting cold if she left them for a minute. She rushed out of the nest box and back several times without stopping to eat, and seemed greatly disturbed. Suddenly she rushed up to her one remaining young of the previous litter, then 22 days old, well furred, and nearly half grown, seized it in her mouth and carried it into the nest, and leaving it with the tiny naked babies, returned to the food. The foster mother soon reappeared at the breakfast table, but was instantly grabbed up, rather roughly and with many squeaks carried back into the nest, where this time it remained while the real mother finished her breakfast. . . . When a half-grown female jumps and squeaks at an old male, he cringes or runs, for he knows that her teeth are sharp, and that she will not hesitate to use them. If he comes too near her newly born young, the mother will sometimes punish him severely before he can get out of reach. If the very young are left unguarded, the males or other members of the family will often kill and eat them or sometimes wantonly bite and kill

them all before their mother returns. In crowded cages it is difficult to prevent the young from being killed, but the mother is a model of care and solicitude, ready to fight to the last for them and to use all her intelligence and energy in their protection."

LEMMING VOLE. The lemming voles are probably as solicitous of their young as are the meadow mice. Burt ('28, p. 214) cites the following experience with *Synaptomys*, which is typical of microtine behavior.

"There were five young in the nest. On returning the following day the young were found to be still in the nest, but on the third day, they were gone. The parent had evidently removed them to another place when she learned that they had been molested."

POPULATIONS

The Malthusian premise would lead us to expect that there is at all times a tendency for the population of meadow mice to live up to the limit imposed upon them by the quantity of food available. In ordinary times this limit is not even approached, as the factors of enemies and probably disease keep their spacing greater. The total population in any area is determined by a combination of factors. Among these we may list as probable, at least, the following:

Climatic conditions:—*Sunshine*: total amount; *precipitation*: total amount and distribution; *temperature*: distribution of extremes; *season*: severity and length of winter.

Enemies:—*Vertebrate enemies*; *parasites* and *disease*.

FOOD:—*Total amount available* (a reflection of climatic conditions); *competition for*, with other species.

Space:—*Sufficiency of*; *competition for* nesting sites, within and without the species.

When one inhibiting factor is lifted for a sufficient period, the population increases until another inhibiting factor checks it. If a series of conditions favor increase over a period of a year or more, the populations swell with marked rapidity until, perhaps, their numbers far exceed those which can be supported by the available food supply. At such times migration, enemies and disease rapidly reduce the ranks of the species until the population is far below the mean.

If one calculates the possible increase in population of mice over any given area, assuming that every female gives birth to an average litter as soon and as often as possible, living at least to middle age, one inevitably develops the picture of a solid column of mice, of the diameter of the area, and rising upward at a startling rate of speed.

One of the saner estimates was developed by Hinton ('18, pp. 24 and 61) for the rats of England. Starting with the assumption of a population of 40,000,000 rats on January 1, an equal distribution of sexes, and half of the number for one reason or another being unable to breed, there is a foundation of 10,000,000 pairs upon which to base the figures of increase. It is then assumed that 95 per cent of the 10,000,000 pairs would die in equal monthly instalments during the year; that each pair of rats surviving long enough has six litters per annum; and that each litter contains on an average eight young. Some of the young die at birth—fifty per cent, it is assumed. Of the survivors, many would never have a chance to breed, and this is assumed to apply to fifty per cent of them, or twenty-five per cent of all born. Those that have a chance of breeding have also to die, and, as in the case of their parents, a natural mortality is assumed to account for ninety-five per cent of these, reckoned from the moment of their birth. Young rats are assumed to breed when four months old, and at the same rate as their parents. The assumptions made above are also made in the case of succeeding generations.

To summarize the possible rat population on December 31, 1918, the following table is given:

	<i>Breeding pairs</i>
Survivors of Capital Stock.....	500,000
Survivors of Generation 2, Litter 1.....	1,291,674
Survivors of Generation 2, Litter 2.....	2,400,000
Survivors of Generation 2, Litter 3.....	3,050,000
Survivors of Generation 2, Litter 4.....	3,150,000
Survivors of Generation 2, Litter 5.....	2,800,000
Survivors of Generation 2, Litter 6.....	1,900,000
Survivors of Generation 3, Litter 1a.....	3,600,000
Survivors of Generation 3, Litter 1b.....	3,600,000
Survivors of Generation 3, Litter 1c.....	3,080,000
Survivors of Generation 3, Litter 2a.....	3,900,000
Survivors of Generation 3, Litter 2b.....	3,700,000
Survivors of Generation 3, Litter 3a.....	3,900,000
Survivors of Generation 4, Litter 1a-a.....	4,270,000

Pairs with a chance of breeding possibly living on

December 31, 1918..... 41,141,674

About the only useful purpose of such an estimate is to bring out the fact that among the rapidly breeding rats and mice there is at all times the potential menace of a serious plague, and that the utmost use of all natural checks must be made at all times.

Climate influences the reproductive rate directly and indirectly. Though breeding throughout the entire year, reproduction in the coldest weather is greatly retarded or in most situations virtually abandoned. Continuous hot weather seems a bar, too, for meadow mice are not found in the tropics. Indirectly the mice are influenced by the weather, which determines the amount and to some extent the sort of cover and food available. Without suitable cover the nests and runways are exposed, and the mice too generally subject to attack to thrive in large numbers.

The quantity and quality of food available is doubtless a great controlling factor. Bailey ('24, p. 530) subjected some of his caged mice to reduced rations, with the following result: "A group of 9 mice, 5 females of breeding age and 4 males, kept in roomy cages and starved for 36 days until hungry, thin, cross, and squealing like half-fed pigs, showed no signs of breeding until at the close of the period when the quantity and quality of their food had been brought up to a satisfying point. The females, fighting the males away, kept them constantly cowed and in fear of their lives, and actually killed and partly ate one old male, the largest animal in the cage. They also killed and ate one quarter-grown young at the time when famine was sorest. As their food was increased and changed to more nutritious quality the females rapidly yielded to male attention and all were quiet and contented again. Even for this short period, others in cages where well fed had raised one family of young and had the next well under way. . . . The three litters of young afterward born to the starved females numbered only 3, 4 and 5, while at the same time, in cages well supplied with food, 5, 6 and 8, were the usual numbers."

The records of Slonaker and Card ('23a, '23b, '23c, '23d) have shown that among white rats kept on a diet restricted to vegetable substance the following are some of the effects resulting; their tendency is to lower the reproductive rate:

1. Restricted diet caused a delayed pubescence ranging from 40 to 92 per cent of the normal. The effect was more pronounced on young immature rats than on older immature animals.

2. Pubescence in young males was delayed more than in young females.

3. The average age at the menopause of all restricted feeders was not greatly changed from the normal, but in young animals mated at the age of pubescence it occurred much earlier in life.

4. The period of sexual activity of the restricted feeders was decidedly shorter than normal, being most marked in young animals, due both to delayed pubescence and an earlier menopause.

5. The restricted diet caused an increase in sterility more than four times the normal. The percentage of sterility was greater in the females than in the males.

6. Animals longest on the restricted diet showed the greatest effect.

7. The animals lost the power of reproduction by the third generation, and the line of descent became extinct.

8. Animals still capable of reproduction were restored to nearly normal condition by an omnivorous diet.

9. In control rats the mortality of the young was greatest in the older litters.

10. The restricted diet caused an increase in the mortality of the young.

11. The mortality of the young was greatest in the first litters, less in the second, and least in the third litters cast by parents from omnivorous stock placed on the restricted diet. This indicates a possible adjustment to the inadequate diet, which required about one-eighth of the average life-span of the rat, and appeared to result in more resistant or stronger young.

12. The mortality of the young of the second generation matings of the restricted feeders was 100 per cent.

13. Cannibalism was influenced by the diet. In general, it was more prevalent in the animals deprived of food from animal sources.

14. A sudden change from the omnivorous to the restricted diet caused a marked increase in cannibalism in the first litters. The last litters had the least percentage of young eaten. This suggests that some adjustment had been made by the parents, which appeared to reduce this craving for food of animal nature.

15. The general effect of the restricted diet was to greatly reduce the proportion of males. With the exception of one group, the males ranged between 84 and 97 to 100 females.

Though the rats on which these experiments were conducted are generally more omnivorous in their habits than are meadow mice, the latter, too, will normally feed on animal matter as chance offers. Under special famine conditions there is likely to be a similar reduction in the birth ratio.

Spacing, particularly in times of ebb and flow of their numbers, is apparently important in population control. If the mice are stranded, out of the reach of mates, breeding stops. If the mice are crowded, then there is likely to be a scarcity of food, and the individuals are discontented. They will not then breed at capacity, for the females fight off the males to the point of causing them serious injury or even

of killing them. Miller ('11, p. 630) has demonstrated that under crowded conditions fifty per cent of newborn Norway rats will be eaten by their mothers. Among microtines in cages, the males will often eat the young. Possibly they do this in nature also.

MOUSE PLAGUES

No species of animal remains constant in its population. At all times it must be either on the decrease or increase. A static condition is impossible, for too many changing factors are at work to produce fluctuation. Some species of animals have marked seasonal cycles of population, while other cycles extend into scores of years. In small, rapidly breeding mammals, such as mice, there are annual cycles, cycles extending into about three and one-half years, and seemingly more obscure cycles of about eleven years. Plagues of mice may be merely accentuated peaks of normal cycles or may be disharmonious outbreaks due to unusual local conditions. For example, it is quite possible for a mouse plague to be initiated by an overzealous campaign against carnivorous mammals, hawks, owls, and snakes. It happens, too, that mice, which have become established in a newly opened up area, formerly uninhabited, break out in a most startling fashion. Such conditions have led to mouse plagues in Nevada, California and Washington, where irrigation transformed deserts and drainage removed a lake. Here there is food and shelter in abundance, and little interference from enemies, so that their ranks soon outstrip the accommodations.

Nash ('08, p. 86) writes of the overflows of mice that are chiefly annual in occurrence and characteristic of the northeastern United States: "When for any reason the low meadows become unable to maintain the number of voles bred in them, the surplus will move out and spread all over the country, establishing themselves chiefly in the hay and grain fields, where they find favorable conditions during the summer. Food and shelter are everywhere, and their natural enemies, which should keep them in check, having all been killed off, these prolific creatures multiply even more rapidly on the cultivated lands than they would in their original habitat. In winter, however, conditions are not so favorable to the voles in the cultivated districts; the crops having been removed leaves the fields comparatively bare and devoid of shelter except in the long grass and weed grown fence lines and here they take refuge, an old sunken rail fence being a favorite stronghold and an orchard in which a rank cover crop is left standing forming a perfect paradise for these secretive vermin.

Under cover of the decaying vegetation in such places they drive a network of runways in every direction, secure from the observation of all but the creatures specialized by nature to prey upon them."

The longer cycles of populations are, however, the more interesting ones, and apparently these are not self-made periods. Elton ('24, pp. 119-161) has developed most thoroughly an explanation that will in all probability pave the way to a better understanding of the problem. His data have been extended to many groups of animals, but I shall quote him only in his conclusions concerning the microtines. He observes: "The sun varies about 5 per cent in its output of energy, and this variation has now been definitely proved to affect the earth's climate."

It may be added here that, according to Huxley ('27, p. 45), "The energy radiated from the sun is greatest at sun spot maxima, and least at sun spot minima. The yearly path of storms varies with the sun spots, returning to the same area about every eleven years. This has, too, been correlated with a change in total precipitation, affecting most strikingly the animals and plants of semi-desert regions."

To return to Elton (*loc. cit.*), "The number of sun spots has been observed regularly for over a hundred and fifty years, and these have a well-marked period whose average is 11.2 years, but which actually varies from nine to thirteen years in length. Also, although the minima all approximate to zero, the maxima vary in size, so that there is a well-marked major sun spot periodicity shown by the line joining the maxima of the 11-year periods. . . . Huntington and Douglass have shown that the red-wood tree (*Sequoia*) bears a very clear record of past climate in its annual rings, and they have been able to carry this record back three or four thousand years. The trees respond to changes in outer conditions of climate by varying the amount of growth of the wood, and if a large number of trees are measured and the rings of individual years compared, very accurate curves can be constructed. Here again there is a well-marked 11-year period coinciding with that of the sun spots. There are also longer periods. Similarly an 11-year cycle is shown in certain trees from Germany. . . . Changes in the level of Lake Victoria, and some other Lakes are correlated in a very marked way with the sun spot period (*c. g.*, a correlation coefficient of $+0.87$ between Lake Victoria level and sun spots). Here the level is the resultant of rainfall and evaporation, and there is thus an approach to the degree of integration of climatic factors which a living organism is capable of attaining. . . . The amount of variation in temperature on the earth

between sun spot maxima and minima is about 0.6° C. in the tropics, and less as one goes further away from the equator, and this is quite enough to be important. It represents from $1/10$ to $1/20$ of an ice-age, so to speak. A change of 0.5° C. will shift the isothermal line about eighty miles horizontally, and this is obviously enough to have great effects on animals and plants. It is important to note that a variation in the meteorological observations which may appear quite small, may have enormous effects on living organisms. . . . It is clear that the causes of [lemming] fluctuations might lie either with the lemmings themselves or with their environment. It is possible to conceive that there might be some rough natural period in the increase of lemmings' numbers (in the sense of having an increase in their 'bank balance' of numbers every year), which was terminated after a few years by migration and disease following upon overpopulation, and that the population was thus reduced and the process started all over again. A little consideration will show that such an explanation of lemming periodicity is quite untenable [though plagues of mice in France are likely of this nature (Elton, '27, p. 137)]. It is inconceivable that such a process could cause synchronised maxima on the various mountain blocks of southern Norway, which as far as lemmings are concerned, are isolated from one another, or again in the different districts of Scandinavia. When we find further that the lemming maxima are practically synchronous all over the arctic regions and the mountains of southern Scandinavia, any such 'natural rhythm' becomes out of the question. Of course the natural rate of increase is a very fundamental factor in determining the size of periodicity into which the fluctuations will fit. The cause of the periodicity must therefore lie with the environment, and here the only possible factor which is acting in a similar way all over these regions is climate. We do not know how this climatic factor acts, whether directly or indirectly, through plants, or other animals, but there can hardly be any doubt that we have here to look for a periodic climatic effect whose period is about 3.6 years on the average, and which acts over the whole of the arctic regions and in the Norwegian mountains. . . . It is plain . . . that mouse plagues have occurred about every eleven years or multiple of eleven years, and that they seem to come round about the sun spot minimum. This is, of course, only an indication and does not prove much. But in view of other evidence we may say that there is usually a marked maximum in the numbers of mice somewhere every eleven years or so. . . . Now in the case of the mice, there are four main factors which are thought to affect them in an important

way. Firstly, mild winters favour them, and leave a larger stock to start the next season's population. Secondly, better physical conditions during the breeding season. Thirdly, abundant food supply at any time, but especially in the breeding season. This would be the effect of climate favouring plant life in some way, *e.g.*, big crops of beech-mast or acorns. Fourthly, a favourable growing season leaves plenty of plant cover in the winter, which gives the mice protection from their enemies. There must, of course, be other factors as well. But the point is that not only are all these factors connected with climate, but the last three are all the result of the same kind of climatic complex during the breeding season."

History of Mouse Plagues. Before considering the consequence of mouse plagues, let us first review briefly the history of a few of them.

"In the past," according to Lantz ('06, p. 364), "meadow mice have appeared in certain localities in such vast numbers that they inflicted serious damage upon many of the products of husbandry. Their appearance has sometimes been so sudden as to be regarded as miraculous. Plagues of field mice are recorded in the Bible, and in the works of Herodotus and Homer refer to a plague of mice during the Trojan War. The Greeks considered the animals so important that they incorporated into their religious system a mouse god, whose aid they invoked to avert plagues of mice. [The people of Crete saw in these plagues a manifestation of Apollo's displeasure and made human sacrifices to appease him (Regnier and Pussard, '26a, p. 387)].

"Invasions of field or meadow mice have not been rare in Great Britain and on the Continent. J. H. Blasius records outbreaks at Vienna, Magdeburg, Wurttemberg, and other parts of Germany. Stow's Chronicle, quoting Holinshed, states that 'about Hallontide last past (1581) in the marshes of Danesey Hundred in a place called South Minster in the County of Essex . . . there sodainlie appeared an infinite number of mice, which overwhelmed the whole earth in the said marshes, did shear and gnaw the grass by the roots, spoyling and tainting the same with their venomous teeth . . . which vermine by policie of man could not be destroyed, till at the last it came to pass that there flocked together such a number of owles . . . whereby the marsh holders were shortly delivered from the vexation of the same mice . . .' Stow adds: 'The like of this was also in Kent'."

SCOTLAND. (After Maxwell, '93, pp. 122-123). "The present outbreak may be traced back to the year 1888, when the voles were observed to be increasing on the farm of Glenkerry and others in Selkirkshire. In the summer of 1889 the low-lying pastures near Closeburn, in Dumfriesshire, were observed to be infested by enormous numbers of voles, which remained there during 1890, and disappeared in 1891, probably moving up to the hill-pastures, where at the time of the Committee's visit they were swarming.

"On some of the hill-farms this excessive increase was observed as early as the autumn of 1890; elsewhere, however, they attracted no attention till the spring of 1891. The districts principally affected are the hill-pastures in the northwest of Roxburghshire, the south of the counties of Selkirk, Peebles, and Lanark, and the northern part of Dumfries from Eskdalemuir by Moffat to Thornhill. The voles have also appeared in great numbers in the parishes of Dalry and Carsphairn, in the stewartry of Kirkcudbright.

"Mr. R. F. Dudgeon, at the date of his report, estimated that in Roxburghshire, 30,000 to 40,000 acres had been affected, of which he considered 12,000 to 15,000 acres had been rendered useless; in Dumfriesshire 40,000 to 50,000 acres, and in the stewartry of Kirkcudbright 10,000 to 12,000 acres were described by him as infested by voles.

"The Committee received no estimate of the area affected in the counties of Selkirk, Peebles, and Lanark, nor had they the means of verifying Mr. Dudgeon's calculation in respect to the other counties affected, but an area not less than sixty miles in length and from twelve to twenty miles in breadth has been overrun."

SASKATCHEWAN AND ALBERTA. (After Preble, '08, p. 188). "During the autumn of 1900 great numbers of mice probably mainly of this species [*M. drummondi*] overran central Saskatchewan and central Alberta. They entered the storehouses and committed great havoc wherever grain or other food was stored. Immense numbers, many of which were floating down the rivers, were found dead. Throughout the country between Edmonton and Athabaska Landing, we found abundant evidence of their former presence, but fresh runways were only sparingly noted, showing that most of the animals had disappeared. This invasion must have extended over a very large extent of country. I was informed by W. A. Burman, of Winnipeg, that small rodents were so common in Manitoba during the same autumn that fur-bearing animals were trapped with much difficulty, their natural food being so easily obtained."

HUMBOLDT VALLEY, NEVADA. (After Piper, '09b, pp. 5-9). "Damage by field mice [*Microtus montanus*] attracted the attention of the ranchmen in the lower part of Humboldt Valley early in the spring of 1906 and became severe during the following summer. In the fall and winter of 1906-07, the damage had increased until fields here and there in the valley were seriously injured. Extensive ravages first occurred above and about Lovelocks. In May, 1907, fields on the Rodgers' ranch, 5 miles below Lovelocks, were invaded from the lands farther up the valley, the progress of the mice being plainly marked, as the fields above the Rodgers' ranch suffered first. The movement of this great body of mice, it should be noted, was a gradual, scattering progression, first by a few and later by increasing numbers, until the greater part had moved to fresh fields. Numbers, however, finding conditions improved, remained as stragglers in the fields deserted by the main body.

"By October, 1907, a large part of the cultivated lands in this district had been overrun by vast numbers of mice. The yield of hay had been reduced by one-third; potatoes and root crops were largely destroyed; many alfalfa fields were ruined by the mice eating the roots of the plants; and the complete destruction of this, the chief crop in the valley, was threatened.

"The height of abundance was reached in November, when it was estimated that on many large ranches there were from 8,000 to 12,000 mice to each acre. The fields were riddled by their holes, which were scarcely a step apart, and over large areas averaged 150 to 175 to the square rod. Ditch embankments were honeycombed, and the scene was one of devastation. Serious losses in hay and root crops during the summer proved but a slight forerunner of the damage which began in the fall with the disappearance of green food. Burrowing down about the plants, and extending their underground runs from root to root, they either killed or seriously injured the alfalfa. By November they had destroyed so large a percentage of the plants, that many fields were plowed up as hopelessly ruined. They attacked also the roots of trees, seriously injuring or quite destroying orchards. They killed most of the young shade trees planted along ditches, and so completely girdled large Lombardy and silver poplars that in some cases they caused the death of even such hardy trees.

* "By January, 1908, in fields where the mice had existed by thousands the previous summer and fall, comparatively few, possibly 200 to 500 to each acre, remained. The border of the destroyed district was about 6 miles below Lovelocks, and the mice were gradually

moving further down the valley. In the area below this, mice were somewhat in excess of normal numbers and in several centers of abundance had seriously injured fields. Even where most abundant, along the lower border of the affected area, they did not exceed 1,500 to the acre. In the winter they attacked every available food supply. Small willows and even greasewood bushes about the borders of fields were stripped of all the bark within reach, and horse and cattle droppings were gnawed to pieces for the food they contained. Alfalfa roots, however, were the food supply on which the mice were chiefly dependent. . . .

"During this winter season, when the mice were not breeding, large numbers of predatory birds and mammals had steadily depleted their numbers. Mortality, believed to be due to disease, perhaps engendered by the straitened food supply and the severe winter weather, had been everywhere evident. Dead and dying mice attracted general notice, and in opening burrows where no poison had been distributed, dead mice were frequently found in their nests.

"By March 15, poisoning, supplemented by these natural agencies, had destroyed the mice on several thousands of acres where they were most abundant, and the plague was broken before the remaining alfalfa fields had been overrun. In scattered centers, mice continued in destructive numbers until May, but without regaining to any considerable extent by reproduction, they steadily decreased. Later in the summer they had almost disappeared from the valley.

"The scourge of mice swept over about four-fifths of the cultivated area in the lower part of Humboldt Valley. Of about 20,000 acres in alfalfa about 15,000 were so seriously injured as to require plowing and replanting. Over most of this area the alfalfa was replaced by grain crops for the season of 1908, at great expense and loss."

BUENA VISTA LAKE BASIN, CALIFORNIA. (Piper, '28, pp. 538-539). "The house mouse (*Mus musculus*) and the meadow mouse (*Microtus californicus estuarinus*)—widely different in origin, character and habits—had thrived in the basin of Buena Vista Lake, Kern County, California, and, by the autumn of 1926, had increased to enormous numbers in fields of milo maize and barley. That the area of these fields had been long water-covered prior to the summer of 1924, and that the surroundings of the basin are of desert character with few human habitations, somewhat simplified the study of conditions connected with the infestation and migrations.

"On November 24, 1926, a vast aggregation of house mice issued from the basin maize fields. Other aggregations involving many

hundreds of thousands of these rodents emerged from the basin at four or five different points December 8 to 10. A third exodus quite as great occurred January 10 to 12, 1927, when the mice streamed quickly across the intervening desert to the few and widely scattered human dwellings. Ranch houses 3 to 10 miles distant experienced sudden visitation. Stacks of grain, hay, empty shacks, and places long abandoned apparently attracted thousands of the mice. Establishments in the oil fields, including several communities 3 to 6 miles west of the basin, were overrun. On the second night following the start of the main marches, there was a sudden invasion of the towns of Midland and Taft, 8 miles west, and of Monarch and Maricopa, somewhat farther to the southwest.

"With the second rush were intermingled a few meadow mice, and with the third, far larger numbers. The spreading of meadow mice continued through January and February to marginal territory within 3 to 5 miles, and particularly to localities then developing a good growth of grasses and alfalfa (*Erodium cicutarium*). Those invading an agricultural area east of the basin made serious inroads on seeded wheat, and caused anxiety for the safety of crops."

Biological Characteristics of Over-Population in Meadow Mice. 1. *Fluctuations in the population of one species are accompanied by fluctuations in the population of other species:* Thus in the Scottish plague of 1829-30, the hordes, though mainly of *Microtus hirtus*, were also composed of abnormal numbers of the long-tailed field mouse and the bank vole. In a plague of house mice in South Australia and Victoria during 1916 and 1917 (Hinton, '18, p. 41), the native mice also increased their numbers beyond the mean. In the recent Buena Vista outbreak the house mouse (*Mus musculus*) and the meadow mouse (*M. californicus estuarinus*) were present in almost equal numbers, though the numbers of meadow mice are minimized by Hall ('27a, p. 199). Other wild species were said to be present in normal numbers only. Where the food available was chiefly grain, the house mouse predominated; in other areas, *Microtus*.

The simultaneous fluctuation of different species, if it can be correlated with the sun spot cycle, will lend support to this theory of population. In the case of the Buena Vista outbreak, however, it seems that the two maximum populations may be accounted for by the lack of enemies and the abundance of food and shelter without invoking the aid of favorable weather. Piper ('28, p. 557), however, records 1925 and 1926 as "rodent years" in six of the western states.

2. *Fluctuations of the numbers within one species cause fluctuations in other species.* The relation between mouse populations and the numbers of their enemies is obvious. To cite a few examples: Elton ('27, p. 139) has shown that in Canada the arctic fox fluctuates with the lemmings, the red fox with mice and rabbits, the fisher with mice, rabbits, "and also fish"[?]. Red and arctic foxes show both $3\frac{1}{2}$ and 11 year cycles, as do the lemmings and mice on which they feed. It is said that at the time of the Scottish plague (Maxwell, '93, p. 131), the short-eared owls which had flocked to the feast bred freely where they were rarely known, produced more than one brood, and had from eight to thirteen eggs in a clutch instead of from four to eight.

Species in competition for food and shelter with the species whose population is waxing, if they are not similarly affected by the factors causing increase, would of course suffer, due to the destruction of cover and sustenance.

3. *In times of mouse plague, enemies flock to the abundant food.* The short-eared owls almost universally appear on the scene at the time of a mouse plague. It is said (Elton, '24, p. 145) that at such times they often stop on migration at places which in ordinary times they do not visit at all: Such gathering is recorded from South America, Texas, Canada, Britain and Norway. Hall ('27a, p. 199) says that at the Buena Vista outbreaks, hawks, owls and ravens were more abundant than usual. He writes: "Named in order of their abundance . . . the hawks noted were: Marsh Hawk, Western Red-tailed Hawk, Desert Sparrow Hawk, and a rough-legged hawk. Barn Owls were abundant, and Short-eared Owls were seen wherever there was terrestrial cover."

Piper ('09b, p. 21) related that in the Humboldt Valley plague, and in other infested localities, the bird and mammal enemies flocked to the scene and did splendid work in aiding in the reduction of the pests.

4. *The year previous to an outbreak, mice are abundant beyond the normal, though the great hordes usually appear with comparative suddenness.* This increase in numbers is sometimes observed for more than one year previous to the plague (Piper, '28, p. 545, and '09b, p. 5).

5. *A migration may take place from the area of overabundance.* In the case of the California plague, Hall ('27a, p. 191) considered it the consequence of deprivation of food both through overgrazing of sheep and the feeding of the mice themselves. This outbreak was characterized by numerous tongue-like waves of migration. Piper

('28, pp. 541-542) records them on the following dates: September 15, southwest, $9\frac{1}{2}$ miles; November 24, west, 3 miles; December 6-8, to the northwest, west and south, the house mice covering 10 miles in two nights, the meadow mice about half this; December 20 to 25, east, $9\frac{1}{2}$ miles; January 10-12 (the heaviest and last migration), all directions. Piper correlates the initiation of the movement with rainfall. He also shows that the course taken by the migrating hordes is strikingly direct, and in the case of the house mice, to human habitations.

Hall ('27a, p. 197) on the contrary states that "The radial migration resulted, at first, in apparently equal numbers of the mice moving outward in all directions. Seemingly, therefore, no choice of destination was made by the mice; perhaps more properly speaking, there was no stimulus or positive attraction causing all of, or even the majority of, the mice to move in one given direction rather than in another." Hall discusses the problem further, saying: "To assume that the movement of one mouse in a given direction acts as a stimulus for another one nearby to do the same, or that this movement at least discourages the latter from going in a different or exactly opposite direction, explains the movement once it is begun. But of course it could not explain the equal movement in all directions from one central point." It would be of interest if someone on the scene of the plague at the time of the migrations could establish the initiation of this movement even with slight flooding, which might have been caused by the rains which Piper mentioned. But is this problem of radial migration quite that which Hall made of it? Piper, who had the advantage of a longer period in the field and more aid for his observations, though arriving after the maximum migration, is probably correct ('28, p. 559) in interpreting the facts as merely very startlingly accentuated normal seasonal migration phenomena in the house mice, between the towns and the maize fields. There is no more likely explanation of the routes taken and the speed with which they were accomplished.

6. *Breeding ceases with overcrowding.* Hall ('27a, p. 196) noted in the California outbreak that no mice less than three-fourths grown were seen (early in January), and this he attributed to the exhausted food supply inhibiting breeding activity. Piper ('28, p. 549) states that in hundreds of house mice which he examined, January 22 to February 10, in this outbreak, there were no signs of breeding. Dr. Clara J. Lynch made autopsies on thousands of mice from the region as late as February 10, with similar results. Piper concluded from all his evidence that breeding ceased about the time



Fig. 188. Norway pine plantation on the border of Kensico Reservoir, New York City water system, showing conditions conducive to mouse injury. Norway pine fortunately is comparatively immune to this sort of damage.



Fig. 189. Dry upland field, Bedford, N. Y. The meadow mice move into this situation in winter and in the more favorable summers.

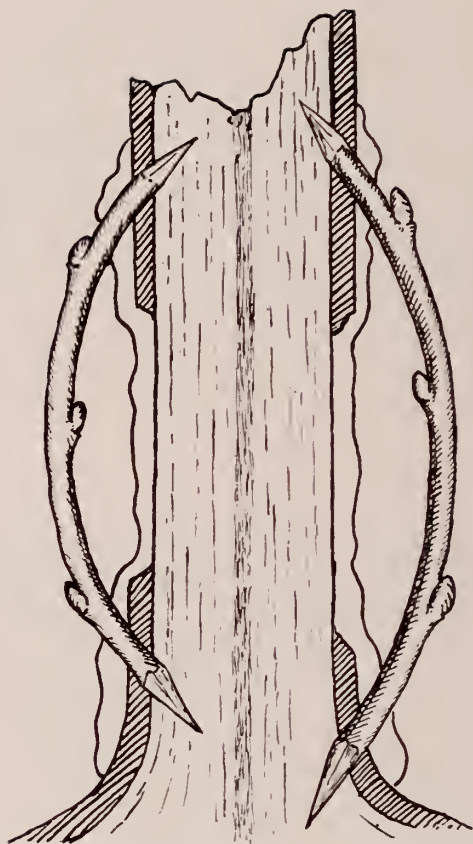


Fig. 190. The method of bridge-grafting a mouse girdled tree. Redrawn from Ballou.

that mouse bands started moving over the basin and migrations had begun. Meadow mice through January were breeding at a strikingly retarded rate. Selle ('28, p. 94) found no mice less than one-half grown in February, and in a large series found but one pregnant female. The work of Slonaker and Card ('23a-d) summarized in the section on breeding habits supports this field information.

7. *The decrease in numbers is sudden.* Plagues usually subside during winter and spring, following their maximum; epidemic disease, predacious enemies, poisoning campaigns and starvation appear to be the factors most commonly acting toward their abatement. There is little information on the ending of plagues unaided by man, for where man has watched, he has also poisoned.

8. *Disease usually appears at the height of a mouse plague, and appears to be the principal factor in causing its subsidence.* It is said, too, that the year of maximum abundance of small rodents in Africa and Asia are years of maximum incidence of human plague (Huxley, '27, p. 48). In the California plague, Hall at the time of his visit (January 13-16) saw no signs of disease among the mice, but Piper found it, January 22-23, among the meadow mice, and it was noted also at later dates. House mice were less affected. Many dead meadow mice were found in their burrows. Wayson ('27) has given a laboratory diagnosis of the disease occurring in this outbreak.

9. *Selection works with increased rapidity in times of over-population, though in general a different set of factors then undergo selection than at other times.* The ability to withstand starvation rations, to withstand the diseases which help terminate a plague, and to travel long distances, might all be factors undergoing selection with crowding. However, we have no proof that these are heritable. In inter-plague times we might expect to find such things as the ability to find mates more operative than under crowded conditions.

10. *The periodical renewal of a vast population from the few remnants of a plague tends towards stabilization of the species.* In times of minimum population there is relatively less chance for uncommon hereditary factors to carry over, so that the older characters which would be present in the greater number of individuals would tend to become better fixed, or in other words, to occur again in high proportion among the members of the next occurring tide.

THE CONTROL OF MICROTINE POPULATIONS

The question of the control of microtine populations varies, of course, with different conditions. Preventive measures may in some sections and some situations need to be kept in operation at all times, whether or not the work of mice is clearly noticeable. A few of the more important of these measures that can be taken for the control of numbers of microtines may be mentioned:

1. The preservation, by legislation and individual cooperation, of the natural enemies of mice. To this end it is of particular importance to leave most hawks, owls, and snakes unmolested, and to encourage the presence of a reasonable number of predatory mammals.

2. The local abundance of meadow mice may possibly, if necessary, be curtailed by the drainage of wet meadows and the periodic plowing of grass lands which give them food and shelter.

3. Cleaning out of weeds and all litter from gardens, orchards, nurseries and fence rows. Sometimes nothing is more effective than this in securing immunity to gardens and orchard trees.

4. Burning of dead grass in meadows and pastures for this same purpose of destroying food and shelter of the mice. This should not, however, be done in late spring or summer as quail and other ground-nesting birds would then be destroyed.

When mice are already doing serious injury other methods must be adopted. If the damage is purely local, that is, confined to one small garden or orchard, trapping may be effective enough. If the mouse activities are extensive, poison may have to be used against them. Irrigated lands are sometimes adapted to wholesale destruction of mice by flooding. These various methods of warfare will be considered separately.

Trapping. According to Lantz ('18a, pp. 8-9), "If mice are present in small numbers, as is often the case in lawns, gardens, or seed beds, they may readily be caught in strong mouse traps of the guillotine type. These should be baited with oatmeal or other grain, or may be set in the mouse runs without bait.

"Trapping has special advantages for small areas where a limited number of mice are present, but it is also adapted to large areas whenever it is undesirable to lay out poison. It is then necessary to use many traps and continue their use for several weeks. If mice are moderately abundant, from 12 to 20 traps per acre may be used to advantage. These should soon enable one to make decided inroads

on the numbers of mice in an orchard, if not practically to exterminate them. For pine mice, the tunnels should be excavated sufficiently to admit the trap on a level with the bottom. A light garden trowel may be used for the necessary digging."

Flooding. In irrigated districts meadow mice may be forced to the ditch banks by flooding the fields. Here poison, dogs, or boys with clubs, may be used to dispatch the congregated mice. Drowning the pests by the flooding of their habitats is not effective, for these mice are capable swimmers, and even the young, as pointed out in the section on Aquatic Specialization, are able to withstand prolonged submersion.

Poisoning. The effectiveness of poison against mouse populations is established. Both locally and in time of plague it proves most useful. In all the recent North American outbreaks, various poisons have been used. In general, however, poisoning should not be attempted without careful study of the methods recommended. Instruction by a properly trained man is preferable. Aid may usually be secured from county, state or federal agricultural bureau agents.

Couch ('28, pp. 73-74) credits the distribution of 75,986 pounds of poisoned grain during a two-year outbreak of *Microtus* in Washington, with the reduction of the pest in that instance.

Such methods are constantly in use against prairie dogs and ground squirrels, which the stockmen and farmers are so anxious to eradicate. The Biological Survey and cooperating parties had, in 1920 (Bell, '21, p. 431), treated 18,000,000 acres of farm and range lands, requiring the use of over four tons of strychnia. I have no figures on similar work against mice, but doubtless if they were available they would be equally startling.

While it is not the purpose of this paper to deal at any great length with the various poison methods used in the extermination of mice where they are found to be too numerous, yet it is deemed advisable to include a summary of a few of the more important ones.

The use of yellow phosphorus (occasionally used in solutions of carbon bisulphide on wheat) is to be discouraged even though it is cheap and effective, for the phosphorous is inflammable and explosive, as well as destructive to other animal life. It has been known to set fields and farm buildings on fire, where used against mice. In the Nevada outbreaks of 1907, great numbers of birds, skunks and domestic cats were killed by this poison, and fatal poisoning of livestock also was frequent (Piper, '09b, p. 8).

Calcium cyanide dust applied with blowers was used in barns, cribs and granaries for the quick destruction of mice in the 1926-27

California outbreak. It has, however, the disadvantage of not reaching mice that are in the tightly packed centers of such grain bins.

Strychnia sulphate is the most useful of all the poisons. In times of plague it is best used on steam rolled barley or alfalfa, for when it is on whole grain, it is taken by many birds. There is little danger in its use, for the strength necessary to kill mice is not sufficient to kill cattle; in a few days its effectiveness is gone, and the poison washed into the ground.

A few of the most useful formulae are:

No. 1. After Dearborn ('11, p. 2).

Wheat	1 bushel
Water	1 quart
Starch	2 tablespoonfuls
Saccharine	2 teaspoonfuls
Strychnia (pulverized).....	2 ounces

"Add the starch, saccharine, and strychnia to the water, heat to boiling, and stir constantly after the starch begins to thicken. When the starch is fully cooked, stir it into the wheat, every kernel of which should be coated. A galvanized iron washtub is an excellent mixing vessel, especially as it is easily cleaned. Either the sulphate or the alkaloid of strychnia may be used.

"During rainy weather it is better to substitute melted tallow for the starch solution as a coating medium. In this case, the wheat should first be slightly warmed and the saccharine and strychnia added; and then the tallow applied, in the ratio of a quart to a bushel of wheat."

No. 2. After Dearborn (loc. cit.).

"A much more attractive bait, and one much easier to prepare, is oatmeal, or rolled oats, the sole objection being its cost, which considerably exceeds that of wheat. Excellent results have been obtained with poison prepared as follows:

Rolled oats	25 quarts
Strychnia (pulverized)	1 ounce
Saccharine	1 teaspoonful
Water	6 quarts

"The strychnia and saccharine are first added to the water, which is then mixed with the oats to produce a thick dough. This dough may be distributed by the aid of a spoon or small wooden paddle, a piece the size of a small marble being put in each place." It should be distributed immediately, as it is subject to fermentation.

No. 3. After Mills ('28).

Gloss starch	1 tablespoonful
Water	1 pint
Strychnia (powdered)	1 ounce
Baking soda	1 ounce
Corn syrup	$\frac{1}{4}$ pint
Glycerine	1 tablespoonful
Whole wheat	12 quarts
Melted beef fat.....	1 cup
Paraffin	$\frac{1}{3}$ cup

Mix the starch in $\frac{1}{2}$ cup cold water, and stir into $\frac{3}{4}$ pint of boiling water. Continue boiling to make a thin clear paste. Mix the strychnia and baking soda and stir these into the paste. Add corn syrup and glycerine. Apply the mixture to the wheat, mix thoroughly and let dry. Warm the poisoned wheat thoroughly and apply the beef fat and paraffin in the hot mixture.

"To prevent all danger of poisoning grain-eating birds, twigs of apple trees as a bait may be substituted for wheat. The twigs or sprouts, cut 6 to 8 inches long, are dipped into the liquid poison, or the poison applied to them with a brush, and then sparingly scattered near the base of trees, or at the mouth of mouse burrows." (Lantz, '06, p. 374).

THE DISTRIBUTION OF POISONS. Poisoned grain, meal, or other material should be distributed in quantities not exceeding a teaspoonful at a place over the infested area. This should be placed carefully in mouse runs, the entrance to burrows, or better, under shelters as brush piles, straw, boards, or stone heaps. Old tin cans with their edges pressed closely together, milk bottles, or small drain tiles may be used. In orchards the milk bottles or tin cans should be left out over winter. Simple poisoning stations can be made with narrow pieces of board, and a small piece of tin arched over. These methods are of utmost importance to prevent all danger of poisoning birds and stock.

"Mice and chipmunks are more easily poisoned in spring, when food is scarce, than when seeds and fruits are ripe and insects plentiful. It is advisable, therefore, to distribute poison early in the season regardless of the time of planting seed. When seeding is to be done in summer or autumn, the rodents should be destroyed over a somewhat larger area than is designed to be seeded, in order to prevent invasion from surrounding territory." (Dearborn, '11, p. 4.)

The Use of Virus Against Mouse Plagues. The Danysz virus was first used in Thessaly in 1892-93 by Dr. Loeffler, and it has been used with success in a number of districts in Europe since then. In the Humboldt Valley outbreak in this country some attempts were made to use advertised bacterial preparations, but as they were not properly distributed their success was only partial.

The use of the Danysz virus (*Bacillus typhi murium*) on a large scale has now been well developed by Doctor Regnier and his associates of the Rouen Entomological Station, and they have successfully checked several outbreaks in France. If their careful and thorough methods were used elsewhere, there might be fewer serious plagues of mice, at least among the voles.

The factors which make for the rapid spread of the *Bacillus typhi murium* are not alone those concerned with the consumption of the culture placed near them. It spreads, too, by the cohabitation of the mice, by their habit of fecal feeding, and their eating the dead of their own kind. Five days after treatment, as many as twelve, eighteen and twenty-four corpses may be found in a single nest. (Regnier and Pussard, '26b, p. 451). It is the habit of *Microtus arvalis* to congregate in nests from September to January, and this aids in the spread of infection.

Several reasons have been given for the failure to adopt these methods in America (Lantz, '06, p. 375): "The high price of the cultures and the somewhat uncertain results in their use have militated against their introduction. Moreover, the high temperature of our summers prevents the successful preservation of the cultures. Added to the above is the fear that under new conditions the organisms may prove infectious to game or domestic animals. . . . Apprehension has been entirely dispelled in Europe, but in the case of other organisms experimented with, it proved to be well founded. Further investigations are necessary before bacterial cultures for destroying mice can be recommended for use in this country."

Practical directions for the large scale production of the "Virus of danysz" are given by Regnier and Verguin ('27, pp. 130-144). The sporadic attempts of others at various times to combat mouse plagues with introduced infection have failed, probably in large part, because they had not the proper technique at hand. However, in view of the risks, which are introduced with the use of infectious diseases, Lantz's caution is laudable.

THE PROTECTION OF FRUIT TREES FROM MICE, AND THE SAVING OF INJURED TREES

Ballou ('09, pp. 59-70) has described a number of methods under this head, and it will add to the usefulness of this bulletin to list them here.

The Soil Mound. "First. Clear away the grass, trash or mulch from the base of the tree for a foot or more in all directions. Second. With the foot, or better, with a 'post tamper,' thoroughly firm the surface of the soil about the base of the tree. This breaks down and fills any runs or burrows that may be just below the surface. Third. With a few shovelfuls of fresh soil or cinders form a small mound (twelve or fourteen inches in diameter at the base and from 4 to 6 inches high) about the stem of the tree, firming the soil well."

The effectiveness of these mounds lies in the fact that they are usually free from snow in winter, and the mice will not expose themselves on these to feed. The mound should be repaired with additions of fresh soil each autumn. Cinders, where available, are recommended for the mounds, for the mice will not burrow through them. The mound method has the advantage of being effective and cheap.

The Wire Screen. This is the most effective of mechanical protectors. While more expensive than many others it is durable, and offers protection against all kinds of gnawers. The screen consists of galvanized wire cloth of one-quarter inch mesh. Rectangular pieces of screen are cut out with tinner's shears and rolled over a section of broom or fork handle so as to form cylinders of proper size to enclose the stem of the tree, with an overlap of about one inch. These cylinders are kept closed by their own tension.

For apple trees the cut screen sections are usually 12 x 24 inches in size.

The Wash. This is a thick paint made by mixing together lime, soap, carbolic acid and sulphur, according to the following formula: "Slack one peck of fresh stone lime with old soap-suds, thinning to the consistency of white-wash. For the one peck of lime add one-half gallon of crude carbolic acid, four pounds of sulphur and one gallon of soft soap. Paint the trunks of the trees with this in late autumn."

Saving the Mouse Girdled Trees. Young trees that have been girdled by mice or other small rodents at the time growth begins in the spring, may frequently be saved by certain methods of grafting. The following methods are described by Ballou (loc. cit.) who also gives the formula for making the "grafting wax."

"If young trees be girdled in late spring just as growth is beginning, they may be successfully treated by binding about the wounded parts a heavy covering of smooth tenacious soft clay. A new bark will sometimes form beneath the clay if the inner bark or cambium be not entirely destroyed. It is safer, however, to insert a few long scions as shown in the accompanying picture." (Fig. 190).

"This is called 'bridge-grafting.' The sap circulation of the tree, cut off by the wound made by the rodents, is resumed through the scions which become a part of the tree—enlarging and growing together until, in after years, only a slight enlargement or 'bulge' on the trunk of the tree thus treated will be noticeable.

"In bridge-grafting, the wounds should be made clean and smooth with a sharp knife, and covered entirely with grafting wax. The scions should be cut a trifle longer than the span to be bridged so that, when they are inserted, their curving form will tend to keep them firmly fixed in position. The two ends of the scions are cut to a thin wedge form. Incisions are made in the bark with a narrow chisel—those above the wound sloping upward and those below sloping downward. Insert the scions firmly and wax heavily and securely all wounds made in the operation, especial care being exercised to press the wax in firmly and neatly about the points of union of scions with the body of the tree. The sectional drawing will show more clearly than printed description the manner of making the 'bridge'."

FORMULA FOR STANDARD GRAFTING WAX. "Melt together four parts (by weight) of resin, two parts of beeswax and one part of tallow. Pour the mixture into a pail or tub of cold water. As the mass begins to cool so that it can be handled, grease the hands with tallow and pull and work the lump of wax until it becomes quite light in color. Form into small balls or sticks for convenient use. This wax will keep in good condition indefinitely."

IN CONCLUSION

We have in the previous pages considered at some length the lives of four lowly mammals which, with their relatives, live over a considerable section of the globe. As a group, they are cursed and poisoned wherever their tooth marks show on plants which man calls his own. One could almost count on one's fingers and toes the people on this earth who have printed anything in defense of the voles, and yet in fair review there seems to be more to be said for them than against them. Man, with the opening up of new country to agriculture, has driven out or so greatly reduced the flesh eaters without making corresponding reduction of the mice, that we on occasion have good cause to be alarmed at the consequences.

Of plagues, we have been comparatively free, though such local outbreaks as those in Nevada and in California have been serious; and numerous lesser hordes in many states have proved temporarily troublesome. With our shortsighted destruction of enemies of mice we may expect further outbreaks of similar nature, for, as Hinton ('18, p. 46) aptly remarks, "The weather may be lenient to rodents, —the carnivores never."

Three-quarters of the meadow mice numbers live in lowlands grown to sedges, rushes and coarse grass, classed by the farmers as waste. In the uplands, their homes are in neglected fields and along fence rows. Within such areas they do no harm. If cultivated sections are not bordered by brushy or rank growths of weeds or other dense vegetation, they will not ordinarily be bothered much by mouse pests, for these do not remain on open ground. It is more the wide distribution of the meadow mice and their occasional local outbreaks that give the group a bad reputation. Most of the time over most of their range, they are wholly beneficial.

The pine mice are another problem. Their range is more restricted, but their underground habits and their frequent and unobserved invasions of gardens and orchards give them an advantage over meadow mice. As a result they frequently cause damage and must be controlled when they become common near human habitations.

The red-backed mice are potentially a menace, particularly to young conifer plantations, but at present they are almost disregarded. Being in the main swamp and forest dwellers, they are likely long to live their useful lives and die unrecognized and unaccused.

The lemming vole's record is clear. We only know that these mice are enlisted in the noble army that converts vegetation to flesh, and

thus do their meagre bit to round out the bill-of-fare of our predacious forces. Even though they should break all precedent and become overabundant, the lemming voles would probably cause but little harm, for their diet, to a greater degree than in the other voles, is restricted to grass.

We cannot quite join those who say there is no occasion for killing meadow mice. Perhaps there should not be, but until we can bring back our hawks and owls, our snakes and flesh eating mammals to a point of balance, we must kill the mice where they are doing real harm. Keep the orchards, the nurseries, and the field borders clean, and these occasions will not be numerous.

It is more to the point rigidly to protect mouse enemies by enforced laws and by education than it is to enter with blind zeal into an anti-mouse campaign the first expense of which is not the last. We cannot avoid the conclusion that there is design in nature, and that we are better off working with it than against it.

LIST OF REFERENCES

- AUDUBON, J. J., and BACHMAN, J.
1854. The Quadrupeds of North America. Vol. 1, pp. 1-383.
- BAILEY, VERNON
1897. Revision of the American Voles of the Genus *Evotomys*. Proc. Biol. Soc. Washington, Vol. 11, pp. 113-138.
1900. Revision of American Voles of the Genus *Microtus*. N. A. Fauna, No. 17, pp. 1-88.
1908. Harmful and Beneficial Mammals of the Arid Interior. U. S. Dept. Agric., Farmer's Bull. No. 335, pp. 1-31.
1920. Identity of the Bean Mouse of Lewis and Clark. Jour. Mammalogy, Vol. 1, pp. 70-72.
1924. Breeding, Feeding, and other Life Habits of Meadow Mice (*Microtus*). Jour. Agric. Research, Vol. 27, pp. 523-535.
1926. A Biological Survey of North Dakota. N. A. Fauna, No. 49, pp. 1-226.
- BALLOU, F. H.
1909. Protection of Fruit Trees from Rodents. Ohio Agric. Exp. Sta., Bull. No. 208, pp. 53-70.
- BARROWS, W. B., and SCHWARZ, E. A.
1895. The Common Crow of the United States. U. S. Dept. Agric., Div. Ornithology and Mammalogy, Bull. No. 6, pp. 1-98.
- BELL, W. B.
1921. Death to the Rodents. Yrbk. U. S. Dept. Agric., 1920, pp. 421-438.
- BENT, ARTHUR C.
1921. Life Histories of North American Gulls and Terns. U. S. Nat. Mus. Bull. No. 113, pp. 1-345.
- BROOKS, ALLAN
1927. Can Hawks Prevent Mouse Plagues? Condor, Vol. 29, pp. 249-250.
- BUCKLAND, JAMES
1914. The Value of Birds to Man. Smithsonian Report for 1913, pp. 439-458.
- BURT, W. H.
1928. Additional Notes on the Life History of the Goss Lemming Mouse. Jour. Mammalogy, Vol. 9, pp. 212-216.
- COPE, E. D.
1900. Crocodilians, Lizards and Snakes of North America. Rept. U. S. Nat. Mus., 1898, pp. 153-1270.
- COUCH, L. K.
1928. Relationship of Predatory Mammals and Birds of Prey to Rodent Life. Jour. Mammalogy, Vol. 9, pp. 73-74.
- DEARBORN, NED
1911. Seed-eating Mammals in Relation to Reforestation. U. S. Dept. Agric., Biol. Survey Cir. No. 78, pp. 1-5.
- DICE, LEE R.
1922. Some factors Affecting the Distribution of the Prairie Vole, Forest Deer Mouse, and Prairie Deer Mouse. Ecology, Vol. 3, pp. 29-47.
1925a. Survey of the Mammals of Charlevoix County, Michigan, and Vicinity. Univ. Mich. Occ. Papers, Mus. Zool., No. 159, pp. 1-33.
1925b. The Mammals of Marion Island, Grand Traverse County, Michigan. Univ. Mich. Occ. Papers, Mus. Zool., No. 160, pp. 1-8.
- DICE, L. R., and SHERMAN, H. B.
1922. Notes on the Mammals of Gogebic and Ontonagon Counties, Michigan, 1920. Univ. Mich. Occ. Papers, Mus. Zool., No. 109, pp. 1-46.

- DITMARS, RAYMOND L.
1907. The Reptile Book. Pp. 1-472. New York.
- DIXON, JOSEPH
1925. Food Predilections of Predatory and Fur-bearing Mammals. Jour. Mammalogy, Vol. 6, pp. 34-46.
- ELTON, CHARLES S.
1924. Periodic Fluctuations in the Numbers of Animals, Their Causes and Effects. Brit. Jour. Exp. Biol., Vol. 2, pp. 119-163.
1925. Plague and the Regulation of Numbers in Wild Animals. Jour. Hygiene, Vol. 24, pp. 138-163.
1927. Animal Ecology. Pp. 1-207. London.
- FISHER, A. K.
1893. The Hawks and Owls of the United States in their Relation to Agriculture. U. S. Dept. Agric., Div. Ornithology and Mammalogy, Bull. No. 3, pp. 1-210.
1895. Hawks and Owls from the Standpoint of the Farmer. U. S. Dept. Agric. Yrbk. for 1894, pp. 219-232.
1909. The Economic Value of Predaceous Birds and Mammals. Yrbk. U. S. Dept. Agric., 1908, pp. 187-194.
- FOSTER, G. L.
1926. Contents of Barn Owl Pellets. Condor, Vol. 28, p. 130.
1927. A Note on the Dietary Habits of the Barn Owl. Condor, Vol. 29, p. 246.
- GRAHAM, S. A.
1928. The Influence of Small Mammals and other Factors upon the Larch Sawfly Survival. Jour. Econ. Entom., Vol. 21, pp. 301-310.
- GRINNELL, JOSEPH, and STOREY, TRACY
1924. Animal Life in the Yosemite. Pp. 1-752. Berkeley.
- HAHN, WALTER L.
1909. The Mammals of Indiana. Ind. Dept. Geol. and Nat. Resources, 33rd. Ann. Rept., pp. 417-663.
- HALL, E. RAYMOND
1927a. An Outbreak of House Mice in Kern County, California. Univ. Calif. Pubs. Zool., Vol. 30, No. 7, pp. 189-203.
1927b. The Barn Owl in its Relation to the Rodent Population at Berkeley, California. Condor, Vol. 29, pp. 274-275.
- HATT, ROBERT T.
1923. The Land Vertebrate Communities of Western Leelanau County, Michigan, with an Annotated List of the Mammals of the County. Papers Mich. Acad. Sci. Arts and Letters, Vol. 3, pp. 369-402.
1928. Relation of the Meadow Mouse, *Microtus p. pennsylvanicus*, to the Biota of a Lake Champlain Island. Ecology, Vol. 9, pp. 88-93.
- HAY, O. P.
1892. The Batrachians and the Reptiles of Indiana. Rept. Ind. Dept. Geol. and Natural Resources, Vol. 17, pp. 409-610.
- HINTON, M. A. C.
1918. Rats and Mice as Enemies of Mankind. Brit. Mus. Econ. Ser., No. 8, pp. 1-63.
1926. Monograph of the Voles and Lemmings. Vol. 1, pp. 1-488. Brit. Mus.
- HOWELL, A. BRAZIER
1927. Revision of the American Lemming Mice (Genus *Synaptomys*). N. A. Fauna, No. 50, pp. 1-38.
- HUMPHREY, F. T.
1927. A Serious Plague of Mice in California. Scientific American, May, pp. 330-331.

HUXLEY, JULIAN

1927. Mice and Men. Harper's Magazine, Vol. 156, (December) pp. 42-50.

KENNICOTT, ROBERT

1857. The Quadrupeds of Illinois, Injurious and Beneficial to the Farmer. Rept. U. S. Commissioner of Patents, 1856. Agric. pp. 52-110.

KING, HELEN D.

1924. Litter Production and the Sex Ratio in Various Strains of Rats. Anat. Rec., Vol. 27, pp. 337-366.

LANTZ, D. E.

1906. Meadow Mice in Relation to Agriculture and Horticulture. U. S. Dept. Agric., Yrbk. for 1905, pp. 363-376.
1907. An Economic Study of Field Mice. U. S. Dept. Agric., Biol. Survey Bull. No. 31, pp. 1-64.
1909. Use of Poisons for Destroying Noxious Mammals. U. S. Dept. Agric., Yrbk. for 1908, pp. 421-432.
1917. Economic Value of North American Skunks. U. S. Dept. Agric. Farmer's Bull. No. 587, pp. 1-24.
1918a. Field Mice as Farm and Orchard Pests. U. S. Dept. Agric., Farmer's Bull. No. 670, pp. 1-12.
1918b. Rodent Pests of the Farm. U. S. Dept. Agric., Farmer's Bull. No. 932, pp. 1-23.

LINSDALE, JEAN

1927. Notes on the Life History of *Synaptomys*. Jour. Mammalogy, Vol. 8, pp. 51-54.

MAXWELL, HERBERT E., and others

1893. The Plague of Field Voles in Scotland. Zoologist, Vol. 17, No. 196, pp. 121-137.

MERRIAM, C. HART

1886. The Mammals of the Adirondack Region, Northeastern New York. Pp. 1-316. New York.

MIDDLETON, A. D.

1930. Cycles in the Numbers of British Voles (*Microtus*). Jour. Ecology, Vol. 18, pp. 156-165.

MILLER, NEWTON

1911. Reproduction in the Brown Rat. Amer. Nat., Vol. 45, pp. 623-635.

MILLS, ERNEST M.

1928. Mouse Control in Orchards. U. S. Dept. Agric., Biol. Survey and Mass. Agric. College., Cir. R-2, pp. 1-2. Amherst, Mass.

NASH, C. W.

1908. The Vertebrates of Ontario. Pp. 1-122 and 5-96. Toronto.

NEEDHAM, J. G.

1905. The Summer Food of the Bullfrog (*Rana catesbiana* Shaw) at Saranac Inn. N. Y. State Museum, Bull. No. 86, pp. 9-15.

NELSON, E. W.

1918. Smaller Mammals of North America. Nat. Geogr. Mag., Vol. 33, pp. 371-493.

PIPER, STANLEY E.

- 1909a. Mouse Plagues, Their Control and Prevention. Yrbk. U. S. Dept. Agric., 1908, pp. 301-310.
1909b. The Nevada Mouse Plague of 1907-1908. U. S. Dept. Agric., Farmer's Bull. No. 352, pp. 1-23.
1928. The Mouse Infestation of Buena Vista Lake Basin, Kern County, California. Bull. Dept. Agric. State of Calif., Vol. 17, No. 10, pp. 538-560.

PREBLE, EDWARD A.

1908. A Biological Investigation of the Athabaska-MacKenzie Region. N. A. Fauna, No. 27, pp. 1-574.

- QUICK, EDGAR, and BUTLER, A. W.
1885. The Habits of Some Arvicolinae. Amer. Nat., Vol. 19, pp. 113-118.
- REGNIER, ROBERT, and PUSSARD, ROGER
1926a. Le Campagnol des Champs et sa Destruction. Ann. des Epiphyties, Année 12e, No. 6, pp. 385-522.
1926b. Des Conditions dans lesquelles se propage la Maladie communiquée aux Campagnols par le Virus de Danysz. Compt. Rend. Acad. Sci., Tome 183, pp. 451-452.
1926c. La Constitution des Magasins de Réserve du *Microtus arvalis* Pallas (Campagnol des Champs) et son Importance pour la Pullulation de ce Rongeur. Compt. Rend. Acad. Sci., Tome 183, pp. 92-94.
- REGNIER, ROBERT, and VERGUIN, JACQUES
1927. Donnée Pratique sur la Fabrication Industrielle du "Virus Danysz" pour Campagnols, en vue de son Utilisation en Grande Culture. Ann. des Epiphyties, Année 13e, No. 2, pp. 130-144.
- RHOADS, SAMUEL N.
1898. "Noxious" or "Beneficial." False Premises in Economic Zoology. Amer. Nat., Vol. 32, pp. 571-681.
1903. The Mammals of Pennsylvania and New Jersey. Pp. 1-266. Phila.
- SELLE, RAYMOND M.
1928. *Microtus californicus* in Captivity. Jour. Mammalogy, Vol. 9, pp. 93-98.
- SETON, ERNEST THOMPSON
1909. Life-Histories of Northern Animals. Vols. 1 and 2, pp. 1-1267. New York.
1925. Lives of Game Animals. Vol. 1, pp. 1-640. New York.
- SHALER, NATHANIEL
1891. The Origin and Nature of Soils. 12th Ann. Rept. U. S. Geol. Surv., Part 1, pp. 213-345.
- SHAW, W. T.
1920. The Cost of a Squirrel and Squirrel Control. Agric. Exp. Sta., State Coll. Washington, Pop. Bull. No. 118, pp. 1-19.
1928. The Spring and Summer Activities of the Dusky Skunk in Captivity. N. Y. State Museum Handbook No. 4, pp. 10-92.
- SILVER, JAMES
1924a. Mouse Control in Field and Orchard. U. S. Dept. Agric., Farmer's Bull. No. 1397, pp. 1-14.
1924b. Rodent Enemies of Fruit and Shade Trees. Jour. Mammalogy, Vol. 5, pp. 165-173.
- SLONAKER, J. R., and CARD, T. A.
1923a. Effect of a Restricted Diet. II On Pubescence and the Menopause. Amer. Jour. Physiol., Vol. 64, pp. 35-43.
1923b. Effects of a Restricted Diet. III On the Number of Litters and Young Born. Amer. Jour. Physiol., Vol. 64, pp. 167-180.
1923c. Effects of a Restricted Diet. IV On the Age of Greatest Productivity. Amer. Jour. Physiol., Vol. 64, pp. 203-209.
1923d. Effects of a Restricted Diet. V On Mortality, Cannibalism and the Sex Ratio. Amer. Jour. Physiol., Vol. 64, pp. 297-310.
- STONE, W., and CRAM, W. E.
1903. American Animals. Pp. 1-318. New York.
- SURFACE, H. A.
1906. The Serpents of Pennsylvania. Penn. Dept. Agric., Zool. Bull., Vol. 4, pp. 113-202.
1908. First Report on the Economic Features of the Turtles of Pennsylvania. Penn. Dept. Agric., Zool. Bull., Vol. 6, pp. 105-195.
- TAYLOR, W. E.
1892. The Ophidia of Nebraska. Nebraska State Bd. Agric. Ann. Rep., 1891, pp. 310-357.

TAYLOR, W. P., and LOFTFIELD, J. V. G.

1924. Damage to Range Grasses by the Zuni Prairie Dog. U. S. Dept. Agric., Dept. Bull. No. 1227, pp. 1-15.

VORHIES, CHARLES T., and TAYLOR, WALTER P.

1922. Life History of the Kangaroo Rat. *Dipodomys spectabilis spectabilis* Merriam. U. S. Dept. Agric., Bull. No. 1091, pp. 1-40.

WAYSON, N. E.

1927. An Epizootic among Meadow Mice in California Caused by the Bacillus of Mouse Septicemia or of Swine Erysipelas. U. S. Pub. Health Reports, Vol. 42, No. 22, pp. 1489-1493.

WYMAN, L. E.

1927. Side-lights on the Mouse Invasion. Museum Graphic (Los Angeles Museum), Vol. 1, pp. 140-142.

THE RELATION OF MAMMALS TO THE HARVARD FOREST

BY ROBERT T. HATT*

*Field Naturalist, Roosevelt Wild Life Forest Experiment Station,
Syracuse, New York*

CONTENTS

	PAGE
Introduction	626
The Harvard Forest	629
Forest Mammal Habitats.....	630
White Pine Stand.....	631
Transition Hardwood and White Pine Stand.....	632
Red Spruce Stand.....	635
Hemlock Stand	636
Plantations	636
Annotated List of the Mammals.....	636
Relation of Injurious Mammals to Important Species of Trees.	645
Red Squirrel Damage to European Larch.....	645
Red Squirrel Damage to Scotch Pine.....	646
Red Squirrel Damage to Norway Spruce.....	648
Porcupine Damage to Larch.....	652
Porcupine Damage to Scotch Pine.....	655
Porcupine Damage to Hemlock.....	655
Microtine Damage to Scotch Pine.....	656
Deer Damage to Ash.....	658
Forest Relations of the Principal Destructive Mammals.....	658
Red Squirrels	658
Porcupine	663
Mice	664
Deer	664
The Influence of Mammals in the Cultivation of Various Species of Trees	665
Larch	665
Scotch Pine	665
Norway Spruce.....	666
Experimental Mixture	668
General Considerations	668
Bibliography	670

*Assistant Curator of Mammals, The American Museum of Natural History, New York City.

INTRODUCTION

Serious damage to the plantations of the Harvard Forest occasioned by feeding mammals had been noted in the winters of 1921 and subsequent years. This damage was brought to the writer's attention during the summer of 1925 when he was engaged in making a study of the red squirrel in the Harvard Forest. With the approval of Professor R. T. Fisher, Director of the Harvard Forest, and Dr. Charles C. Adams, at that time Director of the Roosevelt Wild Life Forest Experiment Station, the present study was undertaken. It was jointly supported by these two institutions.

Mr. Neil Hosley of the Harvard Forest, had previously made a thorough study of the damage done to the plantations by the red squirrels and obtained the most essential information in regard to this injury(Hosley, '25 and '28). His work is particularly valuable since it was possible for him to be in the field at the time the damage was being done, and to extend his observations over several years. The observations of the present writer were confined to the three summer months of one year.

The object of the present study was to ascertain what benefits to the plantations and natural growth forests of this area were attributable to the workings of mammals; to determine what factors were responsible for the loss occasioned by these animals and to suggest possible remedies for the local situation. This investigation was, however, not undertaken as a commercial inquiry but only as part of the policy of the Harvard Forest and the Roosevelt Station to further unbiased research into the problems of forest biology.

Camp was established on the south shore of Harvard Pond for the period from June 20 to September 12, 1925, and all field work was carried on with this camp as a base. Trips to North Ashburnham, Massachusetts, and State Line, New Hampshire, were made to investigate special conditions. During the summer of 1926, while studying the red squirrel in the Adirondacks and the Lake Champlain region many additional observations were made which proved the widespread nature of conditions noted at the Harvard Forest. At other times local conditions were investigated at Greenwich, Connecticut; Millbrook and Bedford, New York; and Englewood, New Jersey.

Because of the limited nature of the investigation little general collecting was carried on so that but scanty information can be given as to the vertebrate fauna of the Harvard Forest. No identifications are given unless the systematic status is beyond question. The

author alone is responsible for the identification of all animals and plants listed.

Five methods of inquiry were adopted, which listed in the order of their importance as to results are: observations on the flora showing evidence of mammal damage; interrogation of local residents; field observation on living animals; experimental feeding of captives; and examination of stomach contents of dead specimens. Of the first it may be said that the most important aspect was the examination of damaged plantations. Other methods were to examine forest trees for evidence, to examine the midden heaps of squirrels, and to search for stored or partly eaten foods of all mammals.

Only plantations of Scotch pine, Norway spruce, European larch and mixed conifers were examined, since the investigations of Mr. Hosley had shown other trees to be immune or negligibly damaged.

When the examination of an individual plantation was undertaken it was first roughly mapped, identified as to number and described. For most plantations, the area, age, planting distance, and height of the average tree was determined. In each case the description included a notation of the nature of adjacent habitats and their suitability for habitation by the mammals predatory upon these plantations. Floral composition, area, and ground conditions were considered.

If preliminary reconnaissance indicated that the damage to the plantation was not uniformly distributed a census of every tree, or alternate trees in alternate rows in the larger plantations, was made and the distribution of such damaged trees plotted in relation to adjacent habitats.

If, on the other hand, the damage was uniform (and this was usually the case as most plantations were small) no attempt was made to plot the distribution but only quantitative and qualitative conditions were noted. In very small plantations it was necessary to summarize the damage on every tree in order to obtain accuracy, but usually sufficient numbers could be obtained by surveying alternate rows, or sample rows at right angles to each other through the plantation.

In describing mouse damage, notes were taken to determine the percentage of trees injured and the percentage of these that died or that recovered.

In studying damage by porcupine, the percentage of trees injured was determined, the percentage completely girdled, the percentage partly girdled and the percentage killed in relation to each of these categories.

Red squirrel injury to larch was plotted in relation to the number with terminal buds clipped, the number with laterals clipped, and the amount of defoliation due to clipping of twigs.

Because of the cyclic growth habits of Scotch pine and Norway spruce and because of the squirrels' work on the terminal buds of branches it is possible to determine for a few years back in just which year the damage was accomplished. It was then determined what percentage of leaders was clipped each year, what percentage of the trees had laterals clipped each year, and, in case of Scotch pine, what percentage of laterals was clipped on a single sample tree for each of the three preceding winters.

Combining all these data the total damage to each plantation could be determined and an estimate made of the chances of survival in relation to mammal damage alone.

The influence of snowfall on the degree of annual damage could be determined in the case of Scotch pine and Norway spruce, if the hazardous assumption were made that the winter rodent population is at all times approximately uniform.

The relation of adjacent habitats to liability to damage, the foraging radius of squirrels, and the effect of size and age of the plantation on its susceptibility to depredations could all be determined in so far as the extent of the data justified the drawing of conclusions.

The author is deeply indebted to all who by their many courtesies and constant aid so greatly furthered the progress of the investigation. Professor R. T. Fisher, Mr. A. C. Cline, and Mr. Neil W. Hosley of the Harvard Forest went to unusual trouble in the establishment and breaking of camp, in furnishing transportation to distant areas, and in generally furthering the work at hand. Mr. Cline has kindly allowed the use here of four of his photographs (Figs. 195, 200, 208 and 209) which better showed tree damage than those taken by the writer.

Doctor Charles C. Adams was extraordinarily generous in the use of his time and energy in establishing the investigation and in seeing to the proper equipment of the field party. Mr. W. A. Dence of the Roosevelt Station always cared for the author's requests from the field with unfailing promptness.

Mr. and Mrs. Rupert Gast on many occasions courteously aided the author in many ways while the investigation was in progress.

THE HARVARD FOREST

The Harvard Forest occupies 2,068 acres in the town of Petersham, northern Worcester County, Massachusetts. The region is a highly glaciated peneplain, characterized by low ridges extending generally north and south. These ridges have a scanty soil covering their granitic cores, while in the valleys there is a deep rich soil which is, however, poorly adapted for agricultural purposes because of the abundance of glacial boulders near and on the surface.

The Petersham area was first settled about the year 1720. Within the next century the native forest had been reduced by clearing to about forty per cent of its former area. The bulk of the inhabitants remained on and near the ridges for protection from the Indians and because farming was easier there. The forests were then principally restricted to the lower-lying areas. The next half century, however, brought about a depopulation of the countryside because of the development of manufacturing along the larger streams, the drain on man power caused by the Civil War, and the opening up of the West, all of which made agriculture in the rocky soil unprofitable. The farms were abandoned, and this once thickly settled area was reduced to half its former population (Fisher, '21, p. 9).

The deserted farms rapidly reverted to nature's control, and trees again returned to the land. White pine seedlings gained root in the unplowed fields and nearly pure stands of this species appeared. Where there were no seed trees for white pine the areas grew up into gray birch, poplar, pin cherry and red maple. Broad-leaved trees gained the ascension in recently cut-over areas, regardless of the original stand.

The land for the Forest was obtained by Harvard University in 1907. Since then it has been under careful supervision. It is thus the oldest managed forest in the United States. The greater part of the area is naturally reforested though some seventy acres of plantation are established.

The aims of the management of the Forest as defined by the Director are to provide a model forest to demonstrate the practice of forestry, to maintain an experiment station for research in forestry, and to supply a field laboratory for students. These objects are admirably attained at this time.

With a considerable outlay in land and money devoted to plantations, it is important to know the relations of all forest animals to the trees, both as a means of determining policies for future guidance and as an aid in settling present unsatisfactory conditions. This paper is the result of but one of the many studies, made principally by entomologists, on the fauna of the Harvard Forest.

FOREST MAMMAL HABITATS

About three hundred acres in the Harvard Forest are occupied by grass land, swamps and ponds, while the balance is covered with natural forests and plantations. With the exception of a few negligibly small areas the grass lands are being allowed to revert to forest or are being planted.

In the Harvard Forest there are no remnants of the original stand. All are second growth types varying from seedlings to mature growth. Characteristic of northern New England, the forest is intermediate in make-up between the northern forests and the central hardwood area. No stands are perfectly pure in type, no one species growing in one locality to the exclusion of all others. Yet there are stands which are dominated by white pine, by hemlock, spruce, gray birch or mixed hardwoods. The bulk of the forested land is, however, covered with intermediate types.

For purposes of forest administration the stands of the Forest have been designated as follows: white pine; pine and transition hardwood; transition hardwood; hardwood swamp; gray birch; pine and gray birch; hemlock; pine, hemlock and transition hardwood; hemlock and transition hardwood; pine and hemlock; larch; and spruce. This classification, unless added to, subdivided, and qualified, would not suffice for use in vertebrate ecology, for the ever important undergrowth varies with the openness and age of the stand, the nature of soil conditions, and lastly, the nature of the surrounding habitats.

As a background for the present study it seems advisable to simplify: to describe the clearly marked types of forest characterized by the dominance of one species, or group of species, and to allow the reader to picture for himself the numerous intergrading conditions. Four principal forest types then present themselves. These are: white pine, red spruce, hemlock, and transition hardwood and white pine. No hardwood stands of sufficient purity to warrant the exclusion of white pine from their descriptive names were found. Gray birch areas while extensive are not considered since they are not permanent in nature, nor economically important enough to warrant recognition here. The nearest stand of virgin timber to the Harvard Forest is at State Line, New Hampshire. About two acres are covered with this old growth, the dominant trees of which are approximately one hundred and fifty years old. The ground slopes away from a sharp dry ridge, covered principally with pine, to a

sphagnum bog in which red spruce is dominant. On the intermediate land grow white pine, red spruce, hemlock and balsam. The pines are the largest of the trees and have grown to a magnificent height, with clear straight stems kept well pruned by the smaller moisture-retaining trees below the forest crown. Under-cover is sparse as little light reaches the forest floor.

White Pine Stand. Tom Swamp Block, Compartment VII, one-half acre, age sixty years: Bounded by lake border, white pine and gray birch; ground very wet, being but six inches above lake level.

Few trees other than white pine grow here, so few in fact that they would be overlooked by the casual observer. These species are: white oak (*Quercus alba*), red oak (*Quercus borealis*), wild red cherry (*Prunus pennsylvanica*), and red maple (*Acer rubrum*).

Shrubs and saplings though not numerous, form a high undergrowth. The following, in addition to seedlings of the trees listed above, constitute this stratum: hop hornbeam (*Ostrya virginiana*), chestnut (*Castanea dentata*), purple azalea (*Rhododendron nudiflorum*), high swamp blueberry (*Vaccinium corymbosum*), and wild raisin (*Viburnum cassinoides*).

The sparse low undergrowth was in late summer composed of the following plants: coral fungus (*Hydnum* sp.), royal fern (*Osmunda regalis*, var. *spectabilis*), cinnamon fern (*Osmunda cinnamomea*), common club moss (*Lycopodium clavatum*), ground pine (*Lycopodium obscurum* var. *dendroideum*), club moss (rare) (*Lycopodium sabinaefolium*), moccasin flower (*Cypripedium acaule*), rattlesnake plantain (*Epipactis repens* var. *ophioides*), bramble (*Rubus villosus*?), wintergreen (*Gaultheria procumbens*), late low blueberry (*Vaccinium vacillans*), star flower (*Trientalis americana*) and partridge berry (*Mitchella repens*).

A stand (Tom Swamp Block, Compartment VI, four acres, age fifty-five years; see Fig. 191) not as pure as the above, but situated on higher ground, is worth description, too, since it is more typical of other white pine stands in the forest. It is bounded by Harvard Pond and a roadway, on the other side of which is a mixed growth of pine, hemlock and transition hardwoods of ages up to twenty-five years.

The crown of foliage in this stand is formed by white pine from fifty to fifty-five years old and from fifty to sixty feet high. The second leaf story of young trees and saplings reach a height of fifteen to thirty feet. Six species of trees compose this

group: white pine (*Pinus Strobus*), gray birch (*Betula populifolia*), white oak (*Quercus alba*), red oak (*Quercus borealis*), wild red cherry (*Prunus pennsylvanica*) and red maple (*Acer rubrum*).

The undergrowth, three to fifteen feet high is composed of the saplings of the following trees and adult shrubs: white pine (*Pinus Strobus*), few; quaking aspen (*Populus tremuloides*), occasional; shag-bark hickory (*Carya ovata*), occasional; beaked hazelnut (*Corylus rostrata*), abundant; black birch (*Betula lenta*), common; chestnut (*Castanea dentata*), common; beech (*Fagus grandifolia*), occasional; white oak (*Quercus alba*), common; red oak (*Quercus borealis*), common; service berry (*Amelanchier canadensis*), common; black cherry (*Prunus serotina*), common; wild cherry (*Prunus pennsylvanica*), common; red maple (*Acer rubrum*); and high blueberry (*Vaccinium corymbosum*), common.

The ground growth, consisting of plants from those that truly hug the ground to others three feet high, is composed chiefly of the following species: Several unidentified mosses; common brake (*Pteris aquilina*); club moss (*Lycopodium clavatum*); false Solomon's seal (*Smilacina stellata*), abundant; false spikenard (*Smilacina racemosa*); Canada mayflower (*Maianthemum canadense*), abundant; moccasin flower (*Cypripedium acaule*); wild strawberry (*Fragaria virginiana*); running swamp blackberry (*Rubus hispidus*); wild sarsaparilla (*Aralia nudicaulis*), abundant; pipsissewa (*Chimaphila maculata*), abundant; shinleaf (*Pyrola elliptica*), abundant; greenish-flowered wintergreen (*Pyrola chlorantha*); Indian pipe (*Monotropa uniflora*), abundant; false beach-drops (*Monotropa Hypopitys*), abundant; aromatic wintergreen (*Gaultheria procumbens*), abundant; black huckleberry (*Gaylussacia baccata*), abundant; late low blueberry (*Vaccinium vacillans*), abundant; four-leaved loosestrife (*Lysimachia quadrifolia*); star flower (*Trientalis americana*), abundant; partridge berry (*Mitchella repens*), abundant; smooth aster (*Aster laevis*); sharp-leaved wood aster (*Aster acuminatus*); and seedlings of all trees previously listed.

Other plants occurring less commonly are: clintonia (*Clintonia borealis*), bunchberry (*Cornus canadensis*), mountain laurel (*Kalmia latifolia*), trailing arbutus (*Epigaea repens*), columbine (*Aquilegia canadensis*) and white baneberry (*Actaea alba*).

Transition Hardwood and White Pine Stand. Tom Swamp Block, Compartment I, three acres, age fifty years: Bounded by areas more mixed in character. Mature trees forming the crown are: white pine (*Pinus Strobus*), gray birch (*Betula populifolia*), American beach (*Fagus grandifolia*), white oak (*Quercus alba*), red



Fig. 191. Pure stand of white pine, age 55 years, south of Harvard Pond. The trees in the foreground have been artificially trimmed of their lower branches. August 10, 1925.



Fig. 192. White pine, hemlock, and transition hardwood east of Harvard Pond. August 10, 1925.



Fig. 193. Red spruce swamp, north of Tom Swamp. September 3, 1925.



Fig. 194. Red squirrel midden of red spruce cones, typical of those common in the swamp shown in figure 193. September 3, 1925.

oak (*Quercus borealis*), black cherry (*Prunus scrotina*), red maple (*Acer rubrum*), striped maple (*Acer pennsylvanicum*) and white ash (*Fraxinus americana*).

The undergrowth consists of seedlings of these trees, with the addition of the following trees and shrubs: beaked hazelnut (*Corylus rostrata*), chestnut (*Castanea dentata*), sassafras (*Sassafras variifolium*), high blueberry (*Vaccinium corymbosum*), witch-hazel (*Hamamelis virginiana*) and arrow-wood (*Viburnum acerifolium*).

The low herbaceous growth in late summer is characterized by the following species: maidenhair (*Adiantum capillus-Veneris*), sensitive fern (*Onoclea sensibilis*), false spikenard (*Smilacina racemosa*), false Solomon's seal (*Smilacina stellata*), wild bean (*Phascolus polystachyus*), wild sarsaparilla (*Aralia nudicaulis*), shinleaf (*Pyrola americana*), aromatic wintergreen (*Gaultheria procumbens*), four-leaved loosestrife (*Lysimachia quadrifolia*), partridge berry (*Mitchella repens*), bog goldenrod (*Solidago uliginosa*) and sharp-leaved wood aster (*Aster acuminatus*).

Red Spruce Stand. Tom Swamp Block, Compartment VIII, Stand A, forty acres, age eighty years (Fig. 193): Bounded by leather-leaf bog, gray birch, pine and hemlock stands.

This spruce stand occupies a poorly drained swamp area to the north of Harvard Pond. A few glacial ridges break the level of its floor and in effect form islands. These ridges have been recently lumbered and burned over. The gravel ridges and the intermittent stream beds in the swamp form the only breaks in the dense stand of red spruce covering the area.

The spruce stand is about eighty years old though the trees have reached a general height of but thirty feet. The stand is very close and the tree tops form a dense canopy. Trees of a few other species are scattered through the spruce though their crowns cannot cover more than two per cent of the area. In a few small areas adjacent to the clearings larches are conspicuous, and here grow to a height of fifty feet or more. The trees found here are: white pine (*Pinus Strobus*), red spruce (*Picea rubra*), larch (*Larix laricina*), hemlock (*Tsuga canadensis*) and red maple (*Acer rubrum*).

In this stand there is no understory, but a thicket six to eight feet high occurs in a few open lanes that are the results of intermittent streams. The species composing this thicket are: reindeer "moss", Brussels carpet moss, sphagnum, cinnamon fern (*Osmunda cinnamomea*), clintonia (*Clintonia borealis*), painted trillium (*Trillium undulatum*), large blue flag (*Iris versicolor*).

goldthread (*Coptis trifolia*), pitcher plant (*Sarracena purpurea*), sundew (*Drosera rotundifolia*), dalibarda (*Dalibarda repens*), wild sarsaparilla (*Aralia nudicaulis*), bunchberry (*Cornus canadensis*), Labrador tea (*Ledum groenlandicum*), pinxter flower (*Rhododendron nudiflorum*), aromatic wintergreen (*Gaultheria procumbens*), creeping snowberry (*Chiogenes hispida*) and star flower (*Trientalis americana*).

Hemlock Stand. Tom Swamp Block, Compartment VII, one acre: Bounded by lake border; pine; and pine, hemlock and transition hardwood. The ground level of this stand is not more than four feet above the lake level, towards which it gently slopes.

The stand is practically pure hemlock. A very few scattered white pine (*Pinus Strobus*), paper birch (*Betula alba papyrifera*), and red maple (*Acer rubrum*) occur.

The ground cover is marked by the following species: common brake (*Pteris aquilina*), yew (*Taxus canadensis*), clintonia (*Clin-tonia borealis*), trillium (*Trillium* sp.), goldthread (*Coptis trifolia*), dalibarda (*Dalibarda repens*), wild sarsaparilla (*Aralia nudicaulis*), Indian pipe (*Monotropa uniflora*), purple azalea (*Rhododendron nudiflorum*), mountain laurel (*Kalmia latifolia*), aromatic wintergreen (*Gaultheria procumbens*), star flower (*Trientalis americana*) and sharp-leaved wood aster (*Aster acuminatus*).

Plantations. Plantations occupy some seventy acres of the Harvard Forest. Of these, thirty-two acres are in white pine. Red pine occupies fifteen acres; Scotch pine, three acres; western yellow pine, one acre; Norway spruce, seven acres; white spruce, five acres; and European larch, six acres. There is also an experimental acre containing alternate rows of white pine, Scotch pine, Douglas fir, Norway spruce and western yellow pine. With the exception of a few plantations laid out in white and red pines, all of these plantations are very small stands of three acres or less.

ANNOTATED LIST OF THE MAMMALS

The extensive wooded areas support an abundance of wild life, particularly in that section designated as the Tom Swamp Block, which has been set aside as a State Game Preserve.

The components of this fauna cannot be considered typical of the original for some of the larger forms have disappeared or become scarce through the encroachments of civilization, while other forms

such as the porcupine seem to have come in during recent years in response to changed conditions.

The twenty-seven species listed were taken, seen, or reliably reported. A few other forms probably occur but their inclusion here would invalidate the remainder of the list.

Parascalops breweri (Bachman). Hairy-tailed mole. Two specimens. This mole appeared to be common in the forests along the border of Harvard Pond. The specimens taken had drowned by falling into an open well that intercepted the course of a burrow.

The role in forest economy played by this animal probably lies principally in its insectivorous habits and in the continual overturn of soil by burrowing (Grinnell, '24, p. 843).

Sorex cinereus cinereus Kerr. Masked shrew. Two specimens. This shrew is common in the mixed stand forests. A female taken June 29 contained seven embryos with a crown-rump length of 11 mm.

Like the mole its value lies in its insectivorous habits and its extensive burrowing.

Blarina brevicauda talpoides (Gapper). Short-tailed shrew. Seen. Probably abundant, since conditions are favorable.

So far as known the short-tailed shrew occupies an ecologic niche similar to that of the long-tailed shrew.

Myotis lucifugus lucifugus (LeConte). Little brown bat. One specimen. Commonly seen. A captive, during one evening ate the following: one small dragon fly, several mosquitos, two deer flies, three house flies, and two moths. One of the moths was large, measuring about one inch long. At first the bat withdrew from it, but after a moment's delay seized the insect. The bat then hung by its thumbs from the top of the cage, grasped the wire of the side with its feet and by curling its interfemoral membrane and folding its wings so as completely to enclose the moth, proceeded leisurely to feed on the captive insect. Fifteen minutes later the bat dropped the sole remnants of the moth, its wings.

This and other species of bats occurring in the region without doubt play an important part in maintaining a balanced fauna and are of direct value in the destruction of insects harmful to the forest and annoying to man.

Euarctos americanus americanus (Pallas). Black bear. Reported to be a rare visitor. Bears at one time may have played a certain rôle in reducing the population of the deer (killing young fawns, probably) and of smaller mammals, as well as by the effect of its insectivorous habits and its probable dispersal of seed.

Procyon lotor lotor (Linnaeus). Raccoon. Two specimens examined. Tracks seen. Reported common. Little is known of the part the raccoon plays in the life of the forest. In the Petersham area it seems to be principally of interest as a fur-bearer.

Mustela noveboracensis noveboracensis Emmons. New York Weasel. One specimen. Reported abundant. Through its feeding on rodents and birds this carnivore, because of its abundance, is one of the major controlling factors in these populations.

Mustela vison subsp. (Schreber). Mink. Seen. Frequently taken by trappers. This is another species of importance in animal population control and in value to trappers.

Lutra canadensis canadensis (Schreber). Otter. Tracks, slides, dung, etc., seen. Reported a common visitor.

A young female otter was taken alive by William Baldwin, Jr., a local deputy game warden. He seized the otter as it was chasing chickens about their pen in his yard. Mr. Baldwin, who has also trapped many otter, has furnished the writer with many useful notes, partly from memory but mainly from notes written down during the seven months the otter was captive.

The largest otter Mr. Baldwin has taken, now in the Museum of Comparative Zoology, Harvard, weighed nineteen and one-half pounds. This was a very fat individual. Others taken ranged from fifteen to eighteen pounds. One whose dry skin measured fifty-seven inches from tip to tip was considered large by the fur dealers, yet came from an animal weighing but fourteen and one-half pounds.

According to Mr. Baldwin, two or three young are born at a time. They travel with the parents the first year. His captive, a female, was taken on July 5, and was, according to his description, very small, probably not more than one month old. The following January she measured thirty-one inches over all and had a body length of nineteen inches. Her weight at that time was eight and one-half pounds.

Mating behavior is a rough affair according to the manager of the fur farm that purchased the otter. He writes that "these animals never amount to much for breeding purposes if their teeth are gone. Mating with them is more or less of a fight and we have never had any success with any of the weasel family when the canine teeth were missing."

The summer pelage of the young otter was much lighter than the winter coat. Shedding began about October 10, the new coat appearing in patches until about November 15, when the winter pelage was complete.

The calls of this otter were several. One was a short, sharp whistle, such as is often used by people to call dogs. Another, Mr. Baldwin describes as a "cross between the yowl of a cat and a sharp rapid click of a ratchet". A call used only when the animal was running was a low guttural sound repeated rapidly, described best by a *Wunk-Wunk-Wunk-Wunk-Wunk*. Still another call was a sharp hissing bark of fear or anger, much like the similarly used bark of a fox. When hungry the otter would bark once and then repeat this at intervals of a few seconds.

Fish would be picked up from the tank in the enclosure, two or three at a dive, and would be held in the mouth. In feeding she would always hold the fish by its head, inserting one or two toes in the gills, and, starting at the tail, would eat the entire fish, scales, bones, and all. Rabbit and chicken, too, were eaten, though hair and feathers were not relished.

Progression on land was made by hopping movements, such as made by mink, interrupted by sliding whenever this was possible, even on level ground. The otter proved adept at climbing chicken mesh, and even in traveling on the underside of that which formed the roof of her enclosure.

Otter trails in the Petersham area are well worn and kept open the entire year. They form a circuit thirty to thirty-five miles long and are covered about every three weeks, according to Mr. Baldwin. Several trails were examined by the writer. These were only just wide enough for an otter to pass. They ran under low brush and over small logs. The trails always represented about the shortest route between two bodies of water, though in some cases, they would deviate to include a sharp declivity down which the otter might slide. Two of the three points of land in Harvard Pond had narrow low-lying bases. Across each of these the otters kept a partly open trail. The third peninsula was steeply arched and here the otters had five well marked slides which were shared with the muskrats. These five slides ended in the water, in contrast to a few others seen farther inland. Mr. Baldwin informs me that otter slides in snow are common in winter and usually do not end in water.

Fresh otter dung was found in the tracks. It was black, semi-fluid, and filled with fish scales and bones.

Mephitis nigra (Peale and Beauvois). Common skunk. Seen. A not uncommon resident. Skunks aid in mouse, bird and insect control and in all probability affect some plants directly through their feeding. The skunk is valuable, too, as a fur animal.

Vulpes fulva (Desmarest). Red fox. Droppings seen. Reported

common. The fox contributes to the forest life in the same way as most of the other carnivores.

Lynx rufus rufus (Schreber). Bobcat. Tracks seen. Reported as occasionally trapped. The bobcats together with the foxes probably help to control rabbits and other rodents.

Marmota monax preblorum Howell. Woodchuck. One specimen. Common in and near open areas. The stomach of a three-quarters grown young contained, besides much finely ground vegetable matter, the feathers, skin, and flesh of a nestling bird, mutilated beyond the possibility of identification, but presumably of a ground-nesting species. Through such occasional feeding habits as this, and its feeding on herbaceous growth, the woodchuck is an animal of economic importance, though usually not associated with the forests.

Tamias striatus lysteri (Richardson). Chipmunk. Trapped. Abundant in the Harvard Forest. Chipmunks were seen cutting and storing hazel nuts at the same time the red squirrels were likewise engaged. These rodents, while largely feeders on vegetation, also are insectivorous. Like the squirrels they hoard food supplies, but because these are usually placed in stone walls, stumps, and other places where seeds can not successfully grow, their beneficial effect is probably not so great as that of the squirrels.

Sciurus hudsonicus loquax Bangs. Red squirrel. Four specimens. Common. The author's notes on this species are incorporated in another publication (Hatt, '29). In general it may be said that the red squirrel plays perhaps the most important part of all the mammals of the forest in relation to the trees.

Sciurus carolinensis leucotis (Gapper). Gray squirrel. One specimen. Rare. This squirrel is reported to have been common in the past. Its disappearance seems to have been coupled with the extermination of the chestnut, and accompanied, not caused, by the ascendancy in numbers of red squirrels.

A female taken July 28 had mammae distributed as follows: thoracic 1-1; abdominal 1-1, and inguinal 2-2. They contained a small amount of milk.

Glaucomys volans volans (Linn.) and *Glaucomys sabrinus macrotis* (Mearns). Flying squirrels. Reported. It is probable that both species may occur within the Harvard Forest, though the reports received did not make any distinction. Flying squirrels in other areas have been found to feed on the bark of trees in winter and spring and to feed on many species of fruits and nuts. Also, they feed on insects, by which habit they may in some cases directly benefit the trees.



Fig. 195. Twigs of larch clipped by a red squirrel in a plantation in the Harvard Forest. Photograph by A. C. Cline.



Fig. 196. Laterals of twenty-foot European larch whose twigs have been clipped by red squirrels in a previous winter. June 27, 1925.



Fig. 107. The central part of a larch stem showing stumps of twigs winter-cut by red squirrels. August 25, 1925.



Fig. 108. A twenty-five-foot larch defoliated by red squirrels' winter-clipping of laterals. June 27, 1925.

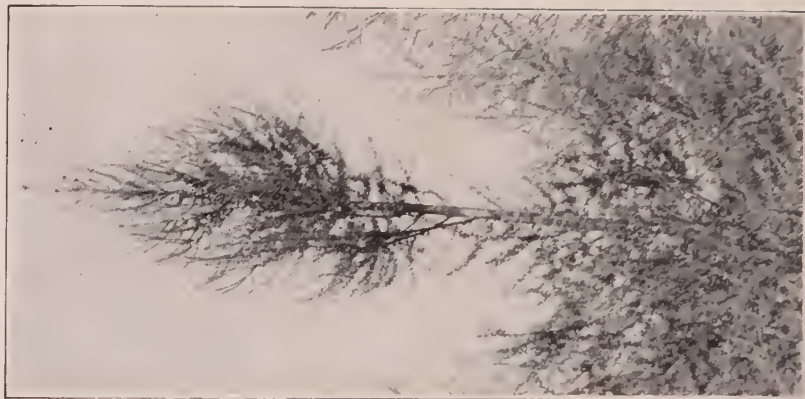


Fig. 109. Another larch showing typical red squirrel injury. August 25, 1925.

Peromyscus leucopus noveboracensis (Fischer). White-footed mouse. Four specimens. Abundant. A female taken July 1 contained four embryos of a 12-mm crown-rump length. Another taken August 31 contained six embryos measuring 6 mm from crown to rump.

A white-footed mouse was found clinging to the vertical trunk of a pine where it had been frightened by a dog. The mouse later ascended to the lowest limb, some fifteen feet above ground. Here it was seen at sunset, four hours later, apparently asleep.

An adult mouse of this species was introduced into a large cage with a pair of red squirrels. The mouse dodged the first savage lunge of one of the squirrels but afterwards disregarded their presence. After a week, the mouse, still alive and uninjured, was sharing the nest box with the captive squirrels.

Clethrionomys gapperi gapperi (Vigors). Red-backed mouse. Five specimens. Abundant. Many red-backed mice were taken in pine forest, red spruce swamp, and mixed forest. Two males and one female were taken in three successive nights in a trap set beside a log in a wet depression in the floor of a pine forest. Several other traps set on drier ground within a two-hundred-foot radius failed to catch a single mouse.

Captives were active sporadically throughout the day and night. One animal was trapped between eight-thirty and nine in the morning.

Mating behavior seems to be a matter of the male forcibly overcoming the female. Two captive males both tried to force a pregnant female newly entered in the cage. She strongly resisted both suitors and succeeded in breaking a leg of one of them as well as blinding him in one eye. This fight was maintained for about twenty-four hours, when the female gave birth to three young. For a day she was caged separately. The young having been killed, the mother was again caged with a single male, the one which she had badly injured. Immediately he attempted to catch her, but she dodged and fought. In the course of a few minutes, however, he was successful. Later in the day they settled down and built a nest which they shared peacefully.

A female taken September 3 contained embryos measuring 3 mm from crown to rump. Five were in the left uterine horn and one in the right.

A captive female gave birth to three young July 4. They measured 30 mm from crown to rump and 39 mm from tip of nose to tip of tail. Body length was 33 mm. The hind foot measured 6 mm. These mice were naked, blind, and but loosely enveloped in their skins.

Males were cannibalistic and killed the young immediately after birth. The mother tried valiantly but in vain to defend the young. When one male would attack her and try to force coitus, the other male would slip in, and, picking up one of the young, commence to eat it. One of these males hung on to a new-born young one so tenaciously that the writer with his fingers on the opposite end had to contest for its possession. When mother and young were removed to another cage she immediately constructed a nest and placed the young, already dead, within it.

The only sounds these mice were heard to make were series of high pitched squeaks that are best described as mouse-like. These were heard mostly when the mice were fighting.

Microtus pennsylvanicus pennsylvanicus (Ord). Meadow mouse. One specimen. Localities that should support a large population of *Microtus* are common in and near the forest. These small rodents are without doubt of considerable importance in their girdling of trees. Their field habitat and their almost strictly herbivorous habits keep them from playing any other part of importance in the forest.

Ondatra zibethica zibethica (Linnaeus). Muskrat. Two specimens. A common resident of the ponds and water courses. Five large embryos were taken from a female trapped July 22. The habits of this animal do not bring it in any direct relation with the forest trees, but it is of importance as a fur animal.

Mus musculus musculus Linnaeus. House mouse. One specimen taken. An established resident at many farms near the forest. One was taken in a pine forest bordering Harvard Pond, though in general it does not invade the forest.

Zapus hudsonius hudsonius (Zimmermann). Jumping mouse. One specimen. It is not known how abundant this mouse is locally nor what its relations to the forest are.

Erethizon dorsatum dorsatum (Linnaeus). Porcupine. Skeleton, sign, etc., seen. Professor R. T. Fisher stated that he had never heard of porcupines in the region until late years and believes that they have invaded the area recently. He also quotes an old hunter of some forty years residence as saying that there were no porcupines near Petersham until a few years ago.

It appears that the only relation of the porcupine to the forest lies in its browsing on trees and occasionally girdling them.

Lepus americanus virginianus (Harlan). Snowshoe hare. One specimen. Reported common. No evidence of damage to trees was seen, though it is reasonable to expect that it feeds at times on the

seedlings of trees, and barks the smaller ones during the winter and spring.

Sylvilagus transitionalis (Bangs). Cottontail. Seen. A half-grown cottontail was seen habitually to feed in the roadway near camp. This animal was coprophagous, which suggested that this habit might aid in explaining the abundance of rabbits in roadways. Their relations to the trees are probably much the same as those of the hare.

Odocoileus virginianus borealis (Miller). White-tail deer. Seen. Trails common. Early one morning a doe, with her twin three-quarters-grown fawns, was jumped on a small island three hundred yards from shore in Harvard Pond. The doe took to water and was followed by the fawns. Half swimming, half walking over the soft bottom, the family soon reached the nearest shore and disappeared. The animals were known not to have been on the island at a late hour the evening previous.

Deer were feeding on brake ferns early in July, stripping the leaves from the fibrous stem. Many seedlings were found in the forests, that appeared to have been stripped of their leaves by browsing deer. It is likely that deer may be responsible for a high mortality among seedlings.

RELATION OF INJURIOUS MAMMALS TO IMPOR- TANT SPECIES OF TREES

Red Squirrel Damage to European Larch. The red squirrel injures larch by clipping off many slender twigs, from which it later eats the buds. The twigs, from six to twelve inches long, are cut close to the trunks (Fig. 197). Usually the clipping of twigs from the main stem is more or less limited to a zone midway up the trunk (Fig. 199), though in more severe cases it may extend the length of the stem and reduce the tree to a nearly bare pole (Fig. 198). A tree with a belted or irregular contour invariably shows numerous short stubs of twigs along the trunk (Fig. 197) and a mat of cut twigs at the base.

After the twig has been cut the squirrel hollows out the buds along its margin and at the tip and then drops the twig to the snow below (Fig. 195). Only rarely are leaders cut, so stems are almost always desirably straight. Red squirrels have not been actually observed doing this injury, but no other local animal would be capable of performing the work in quite the same manner. Almost conclusive evidence lies in a comparison made between some freshly clipped and budded twigs gathered from a plantation after a heavy snow

(mailed to the writer by Mr. Hosley) and some similar twigs budded by a pair of captive red squirrels at the same time. Not the slightest difference was seen between the two. As added evidence the marks of teeth on freshly clipped twigs fit exactly the incisors of a red squirrel.

Injury by twig-cutting is produced during periods of heavy snow-fall. A second cycle of damage occurs in the spring when the buds show first signs of growth (Hosley, '28, p. 46), but at this season the buds only are removed, the twigs being left untouched.

In only two plantations do trees appear to be seriously affected by the cuttings, for the foliage area in other stands is not reduced by more than one-quarter, and this loss is somewhat compensated by the subsequent development of many short twigs bearing dense leaf clusters. The two exceptions (Prospect Hill Block VII v. and w.) have many trees with twenty-five to ninety per cent of their leaf-bearing twigs cut. Here growth must be considerably hampered. Not only are individual trees more badly affected in these plantings but the percentage of trees damaged is much higher.

All the larch plantations are very small, none being more than one and one-half acres in extent. While they do not in themselves support a resident squirrel population, any part of any plantation is easily within reach of the squirrels, since each plantation is bordered on at least one side by a natural stand of mature white pine. All plantations show squirrel damage fairly evenly distributed throughout, as might be expected since the edge of any plantation furthest from the natural forest is within easy traveling distance for a red squirrel.

Red Squirrel Damage to Scotch Pine. The leaders and branches of Scotch pine are stout and offer a good footing to a red squirrel. Probably because of this and the inconvenience of cutting through such a heavy stem, the squirrel cuts off the winter buds at their bases. The inner green tissues are eaten and the large papery husks are dropped to the snow below. A large cluster of buds caps the leader. In most cases each one of these is destroyed and the tree has no method of continuing its growth in height until a new set of buds is formed below the injured whorl. With the coming of the growing season these new buds send forth their shoots at a nearly equal rate, so that instead of a straight leader with a well formed ring of laterals below, there is developed a group of competing branchlets which form a "broom" (Figs. 202 and 203) at the crown of the tree. The annual repetition of such injury together

with similar injury to the buds on branches below the leader results in a growth resembling a bush (Fig. 200) more than a well formed tree (Fig. 201).

A red squirrel has been seen in the act of feeding on the winter buds of Scotch pine (Hosley, '25, p. 455). Examination of the injury revealed conditions identical with those found throughout the plantations. The squirrel traveled through the trees and in consequence left no tracks on the ground below.

Some workers in the Harvard Forest who have observed the injury only in the summer were of the belief that much of the damage might have been due to alternate thawing and freezing in the spring. It was stated by one that a Scotch pine plantation near Syracuse, New York, showed similar bud damage but that there were no squirrels at all in the vicinity. While the writer is not well acquainted with local conditions near Syracuse, it is known that there are red squirrels throughout that region, and it seems more probable that their presence had escaped notice. It is not impossible of course that some other species of squirrel or other rodent was responsible in this instance.

Frost damage to Scotch pine in Europe has been described by Hartig ('95). There it affected chiefly two- to six-year plants (an age group unaffected by squirrels at Petersham) and produced a clinical picture very different from that shown in the Harvard Forest.

No bud injury whatsoever was found in plantations examined through Bronx, Westchester, Dutchess and Essex counties, New York, and in northern New Jersey and southern Connecticut.

Eighty-eight per cent of the Scotch pine at North Ashburnham, Massachusetts, had been deformed by terminal bud injury done by red squirrels. Twenty-eight per cent of all trees had the leader killed but once. Forty-two per cent were twice injured. Twelve per cent had been clipped three times, five per cent four times, and one per cent five times. Injury is still continuing.

The effect produced on a single tree is suggested by a census taken on a typically injured tree on the Harvard Forest. The terminal buds of twenty-eight of a possible eighty-three laterals were removed during the winter of 1924-1925. Twenty-five of a possible seventy-nine were cut the winter previous. This work, however, while producing a tree unsymmetrical and ragged in outline, does not affect the growth or straightness of the main stem. On the contrary, leaf surface seems to be increased because of the numerous adventitious shoots that are produced about the budded stems and the total metabolism for the year is probably greater than before.

Injury is greatest in winters of heaviest snowfall. The writer's data bearing this out were obtained from a single plantation count of damaged leaders and gives figures less striking than those of Hosley who carried his census over five plantations. Damage in the winter of 1922 was fifty-six per cent. The following winter, one of greater than average snowfall, damage was eighty per cent (Hosley, 93.2%). The winter of 1924-1925, with less than average snowfall, had injury reduced to seventy-two per cent (Hosley, 53.6%). Snowfall during the winter 1925-1926 was heavier than in the preceding winter, and, judging by a letter from Mr. Hosley, the injury produced at that time was more extensive than that of the year previous.

Red Squirrel Damage to Norway Spruce. Red squirrel injury to spruce is, as in the case of Scotch pine, primarily the result of trunk distortion rather than defoliation. The terminal bud, which is well protected from above by a cluster of sharp needles, is usually cleaned out from the base, leaving a hollow, normal looking bud sheath. If the bud is not destroyed *in situ* the squirrel may cut off the terminal or a lateral cluster from one to four inches back from the tip (Fig. 206), and carrying it to a secure resting place in the same tree will proceed to feed upon the buds. The most frequently budded points are the leaders and the tips of the first whorl below the leader (Figs. 204 and 205). The tree is saved from serious deformation by the vigorous perpendicular growth of one or more shoots from uninjured buds or branches below the old leader. Occasionally when more than one leader is thus produced (Fig. 207) the competitive growth is wasteful of the energy of the tree. Bending of the main stem of the tree due to the development of a new leader from a lateral bud is not permanent, for the change in angle is not great and disappears with the annual increment in girth.

Squirrels have not actually been observed pilfering the plantations of spruce, but, for the same reasons that it is certain that red squirrels are guilty of larch injury, it is certain that such damage to spruce is to be credited to them also. But unless a definite clipping by sharp teeth is observed it is not fair to accuse the red squirrel for each deviation from straight growth of a trunk, for there are at least two other agencies which cause the suppression of the leader. The first of these is the failure of the terminal bud to germinate; the second, the killing of the leader by the white pine weevil. After about three seasons it would ordinarily be impossible to ascertain which of these caused the damage. Often in case of fracture the



Fig. 200. Scotch pine plantation on the Harvard Forest showing the bushy growth resulting from repeated red squirrel injury. Photograph by A. C. Cline.



Fig. 201. Scotch pine plantation near Speculator, New York, showing no mammal damage. Contrast the straight regular growth here seen with the deformed trees figured above. June 24, 1926.

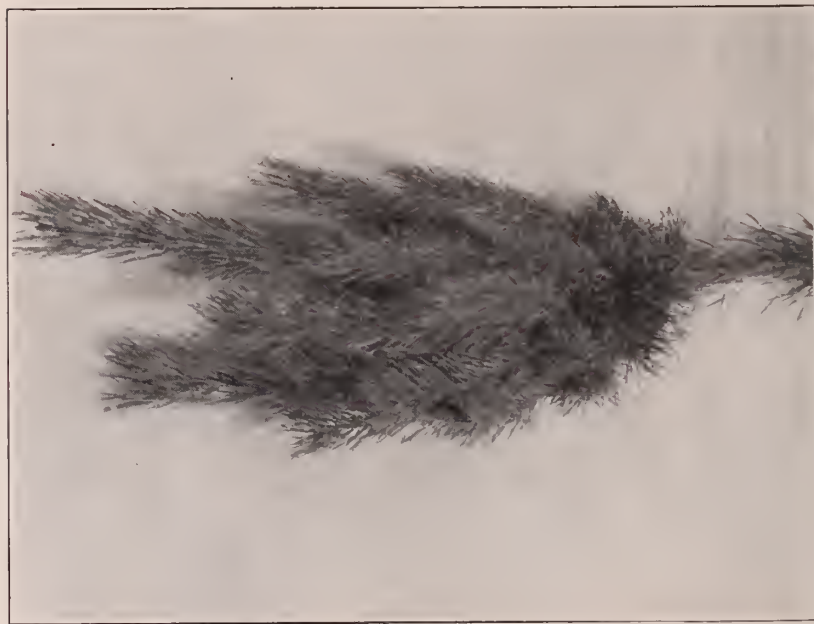


Fig. 202. A "broom" forming the leader of a Scotch pine. This competitive growth of many laterals is due to the destruction of winter buds by red squirrels. September 10, 1925.



Fig. 203. The same "broom" shown in figure 202, with the foliage removed. September 12, 1925.

evidence may be wiped out before examination. Laterals, too, may fail to have the terminal bud germinate, and deviate from their straight course. Some unknown agency occasionally breaks (not cuts off) a tip, but this is infrequent. To be certain that a squirrel hollowed out a terminal bud it should be examined no later than the ensuing spring.

Damage is most severe during the periods of heavy snowfall, as in the case of Scotch pine, according to Mr. Hosley.

Four plantations of Norway spruce occur in the Forest. Of these only two have been injured. The most severely damaged plantation was a fifth-acre stand of ten-foot trees. Here no tree escaped injury. A four-acre tract of trees from ten to twelve feet high showed extensive though uniform damage. The distribution of injury is clearly correlated with the character of the adjacent habitats. To the south a fifteen-acre open heath, blanketed by a dense growth of spiraea, raspberry, blackberry, blueberry, sweet fern and grasses, supports no squirrels. To the west a broad belt is planted to young Norway spruce and white pine. No squirrels would invade from this quarter. To the north a stone fence separates the plantation from several acres of pasture which supports a scattered growth of mature white pine. Possibly a pair (or more) of squirrels lives in these trees and forages on the plantation. To the northeast is a plantation of nine-foot white pine, not a habitat of red squirrels. From the east must come the bulk of the invaders. Here is a natural growth of twenty-five-foot white pine containing a sprinkling of hardwoods. While this stand supports red squirrels it does not appear old enough to furnish an abundance of food. Injury to the plantation proves most severe, as might be expected, on the eastern and northern borders. The squirrels appear to invade from the forest directly and by way of the stone wall. Damage diminishes toward the south to the last twenty rows which are practically untouched. In contrast, the northernmost twenty rows show scarcely a tree that has escaped.

Adjacent to this plantation is a stand of five-year-old Norway spruce which is as yet undamaged, seemingly because of the small size of the trees.

No trace of damage occurred in the fourth plantation. This was a stand of about one acre of ten-foot trees. The reason for its escape from squirrel depredations appears, as was first suggested by Mr. Hosley, to be due to the age and extent of the forest bordering the plantation. The stand was mixed growth from seventy to one hundred years old. Large quantities of cones and nuts are available over an extensive area and it seems practically conclusive that

here alone the squirrels are able to find and store sufficient winter foods; and furthermore here alone is the forest old enough and extensive enough to contain in fullest numbers the natural enemies of the red squirrel.

The effect of heavy snowfall on the amount of injury is borne out by the figures of Hosley, and my own, also, though Hosley's figures ('28, p. 46) show almost six times as much damage to the same plantation as do mine. Mr. Hosley's census was taken in winter, when damage was fresh and cuttings could be seen on the snow. He obtained his percentages by a row count of one hundred trees, while mine, taken in summer when damage was not so evident, were obtained by examining every other tree in every other row. One-fourth of the trees in the plantation were therefore examined, and the entire area was represented. Presumably Mr. Hosley saw the damage more clearly than I, but did not obtain representative figures because of the method of counting. It is probable that the true percentage lies somewhere between Hosley's figures and mine.

The winter of 1924-1925, a year of light snowfall, was accompanied by four per cent injury in this plantation. The winter previous, a season of heavy snowfall, was marked by thirteen per cent of the trees being cut. The winters of 1922-1923 and 1921-1922 showed nine per cent and four per cent injury respectively.

Porcupine Damage to Larch. The porcupine has found European larch to its liking and in winter has invaded the plantations of this species and taken its toll of trees. All injury is done in winter or early spring. To appearances most of it is done from the surface of the snow, or while the animal sits on the lower branches. Due probably to the small size of the larches, the injury is confined principally to the main stem (Fig. 208), from which the rodent eats the bark.

If the tree is but partly girdled, it lives on. When completely girdled two feet or so from the base, all the tree above this banding dies, while below it the branches will retain their vitality. If the tree is completely encircled at the base it usually dies. A single exception to this was found. Here the tree was completely girdled for ten inches along the stem. The tree at this point was three inches in diameter.

Four of six plantations showed porcupine injury. Those which had escaped were the two smallest. In each of the other four, damage was concentrated in a small group of trees along a border adjacent to mature forest, though individual trees scattered through the plantation showed injury. The porcupine is not overfond of roving and seems content to settle itself in a small group of trees.



Fig. 204. The crown of a six-foot Norway spruce with the terminal and lateral twigs cut by red squirrels the winter previous. June 27, 1925.



Fig. 205. The crown of a five-foot white spruce on Valcour Island, Lake Champlain, New York, with the leader cut by red squirrels. August 26, 1926.



Fig. 206. Branch tips of Norway spruce with winter buds hollowed out by red squirrels. January, 1926



Fig. 207. The crown of a nine-foot Norway spruce showing twinning of leaders apparently caused by red squirrel clipping a leader in a previous winter. June 27, 1925.

The plantation showing the heaviest proportion of trees injured or killed by porcupine had twenty-two per cent of the trees affected. Five-eighths of these were killed. The second most serious case showed twenty per cent of the trees girdled. Three-fourths of these resulted in deaths. A third plantation had but nine per cent of its trees touched. Of these, also, three-fourths were killed. The remaining damaged plantation had trees barked to the extent of seven per cent of the total. Approximately three-fourths of these had died.

Compared with the red squirrel, the porcupine does not cause such extensive damage to larch plantations, though where it does attack its work is far more thorough.

Porcupine Damage to Scotch Pine. Scotch pine plantations of the Harvard Forest have not as yet been damaged by porcupines. At North Ashburnham, Massachusetts, there is, however, a privately owned plantation which demonstrated clearly what is to be expected in the Petersham area when conditions are adverse. The only environmental difference the writer could detect between the locality of the injured plantation and that of the uninjured was that the Scotch pine plantations in the Harvard Forest, where they were near porcupine-infested areas, were also close to larch plantations. In these larch plantations the porcupines foraged evidently preferring them to those of Scotch pine. Hemlock, an important porcupine food tree, is common near plantations in both areas.

The porcupines girdle these pines as in the case of other trees. They stand or sit on the ground, snow or a low branch and eat until all the bark within reach is consumed, or until they are otherwise prompted to move. The bark is removed to the wood, so that complete girdling results in the ultimate death of the tree.

No porcupines were in the plantation the middle of July, though some of the damage was not more than a month old. The animals probably feed here throughout most of the year.

A representative census of two hundred trees in the plantation showed thirty-two per cent damaged, while of these but ten per cent were dead, or about three per cent of those in the plantation. The stand, which covers nearly three acres, was planted about 1910.

Porcupine Damage to Hemlock. Porcupines commonly feed on the bark of hemlock, but in only two trees, growing close to each other, was the damage seen to be extensive. It has been previously stated that the advent of the porcupine into this region is quite recent. It may be for this reason that damage has not become serious throughout the forest.

The two trees noted (Fig. 209) grew in a narrow strip of white pine separating two larch plantations. Several larch trees adjacent to these hemlocks had been girdled and killed by porcupines. At the foot of the hemlocks there were several dens in the rocks, which to all appearances had served as habitations for the one or more porcupines which did this damage. It appeared as though this small circle had been chosen as a feeding ground for a long winter, the time probably having been divided between the den and trees within a radius of fifty feet. The injury was perhaps three years old at the time of examination.

The hemlocks were each about twenty-five feet high. The porcupines had not girdled the trunk but had gone out on each branch to a point where it was one-half to three-quarters of an inch thick, and here cut the tip off. Along the branch to this point all lateral twigs had been cut, too, except such as were too large. From many of these main branches some bark had also been removed.

Since the time of damage, small twigs have developed from most of the laterals and in places these form tufts of green foliage which from a distance resemble large beads strung at intervals along the branches. Obviously such complete damage to the tree limits its future growth to such an extent that it becomes commercially and aesthetically valueless.

Microtine Damage to Scotch Pine. Damage to one plantation of Scotch pine in the Harvard Forest and to one near North Ashburnham, Massachusetts, is characteristically microtine, though it could not be determined positively which species had been at work as three microtines probably occur in this area—the meadow mouse (*Microtus p. pennsylvanicus*), the red-backed mouse (*Clethrionomys g. gapperi*) and the short-tailed vole or bog-lemming, (*Synaptomys cooperi*). The habitats bordering the damaged plantation in the Harvard Forest are more favorable to *Clethrionomys* than to *Microtus* and it is the writer's belief that the first of these was responsible for the girdling.

The Harvard plantation showed complete girdling of practically all trees that were injured. It would appear that the mice conserved energy in removing the outer bark by feeding on one tree until all within reach had been utilized. At North Ashburnham girdling was complete in only about twenty-five per cent of the cases. The denuded belt extended from the ground to a height of six to twelve inches. Inward, it continued through the cambium.

The individual tree is damaged in ratio to the amount of girdling. An incompletely girdled tree does not die, but a swelling is pro-

duced in the side opposite the injury, by means of which the food and water supply are maintained to the parts above the injury. Since the bark does not regenerate over the place of injury the tree is destined to die before maturity, provided the injury extends over more than one-half the circumference of the tree. This is because of the resulting weakness of the base. The immediate effect produced is a marked stunting of growth, most severe the first season following injury and diminishing in subsequent seasons.

If girdling is complete the tree usually dies within a few months. In a small percentage of the cases, however, the tree forms a huge swelling above the denuded ring and the transpiration stream is apparently reestablished in the deeper-lying layers (Fig. 210). Such trees do poorly and in most cases die within three years, though a few in the Harvard Forest are still alive eight years after the injury. These trees appear, however, to be now very near death. The weakened non-growing base eventually will determine their fate even though physiologically the trees are able to maintain life. A few other trees that have been girdled slightly above the base have sent all their growth into one of the laterals below the band of girdling. This lateral then turns at a right angle to its former plane and parallels the old dead trunk (Fig. 211). The tree, thus making a last abortive attempt to live even though against the probability that it will be able to establish itself firmly enough by roots to support the new trunk, has lost as many years competitive growth as represented by its age when the mice attacked it. Its one hope is in an already well established root system.

The Harvard Forest plantation was girdled to about fifty-one per cent of its total, twenty-one per cent of all the trees being killed from this cause. The North Ashburnham plantation was fifty-nine per cent girdled, half of this number being killed. The trees in the first case were eight years old at the time of injury. The others were apparently but six years old.

In each plantation injury was local in distribution, adjacent trees being affected rather than scattered trees throughout the stand (Fig. 212). In one of these, eighty-three adjacent trees were killed while approximately an equal number were scattered among the living.

Two other Scotch pine plantations in the Harvard Forest, each about one mile from the one damaged, and approximately of the same age, showed no injury.

Injury to the trees of the Harvard Forest was done in the winter of 1917-1918, though there are no records as to the month or the duration of the activity. The owners of the North Ashburnham

plantation state that the injury there was accomplished about 1916. It is probable that the voles in the years of attack on Scotch pine were in a period of over-population and that crowding caused them to draw upon food resources not ordinarily utilized. The fact that mouse damage was not repeated each winter has given the plantation some chance of continued growth. The mice girdled the Harvard trees during a period of heavy snowfall, and judging from the level of the injury, worked from tunnels in the snow. Mouse girdling of Scotch pine is apparently not uncommon in the eastern United States. The writer has observed similar injury near Katonah, New York, and Greenwich, Connecticut. Silver ('24, p. 5) cites a case in New York of complete girdling of one thousand six-year-old Scotch pines in a five-acre block. This he attributes to *Microtus*. Plantations at South Mountain Park, New Jersey, and at Millbrook and Saranac lakes, New York, showed no injury.

Deer Damage to Ash. During the winter and spring months deer feed on the terminal shoots of ash in young second growth stands in clearings. They clip off branches a half-inch in diameter, and while this does not kill the tree it greatly retards growth, and when thoroughly done produces a bushy growth rather than a straight tree. The damage is general in the forest as the deer are wide-ranging, but is most noticeable in the clearings between Petersham village and Harvard Pond. Such damage does not lend itself to statistical analysis and the extent of damage cannot be easily computed. It is not so serious a matter as the killing of trees in plantations, for there has been no monetary outlay in planting; nor is the entire tree growth destroyed, for numerous seedlings of other species stand ready to take the places of the trees that fail.

FOREST RELATIONS OF THE PRINCIPAL DESTRUCTIVE MAMMALS

Red Squirrels. Squirrel injury to trees in the Harvard Forest is practically limited to the harmful effects of their feeding on larch, Scotch pine and Norway spruce during periods of heavy snowfall. Their attack on larch does not deform the trees, but continued feeding produces defoliation which must seriously retard the growth. Their budding of Scotch pine is often carried to such an extent that the tree resembles a bush more than a well formed pine. The stem deviates from the perpendicular and instead of a single pole there may be several, all vying for leadership at the expense of the tree as

a whole. For lumber purposes the tree becomes valueless. The damage in some plantations is so extensive that the whole plantation as a source of lumber is a loss.

Norway spruce is affected by the loss of the leader and subsequent wasteful competition. The effect caused by budding of laterals cannot be serious in reducing foliage area for the tree sends out new buds near the site of the injury. But the formation of new buds must be at the expense of the growth of the trees, for the early growing period is thus lost.

That squirrels bark maple and other trees during winter and spring in many localities is well recognized, and probably the same source of food supply is utilized in the Harvard Forest, though so far as known it has not actually been observed. In undisturbed areas where food is abundant and the animals are held in check by natural enemies there probably is less injury of this sort than nearer farms and cities where the reverse conditions prevail. That such injury to trees has a harmful effect is yet to be demonstrated.

The red squirrels cut vast quantities of the fruits of local trees and utilize many of the seeds for food, either immediately or at a later time when other food is scarce. Cones of white pine, red spruce (Fig. 194), hemlock and arbor vitae are cut and stored in underground pockets, but the seeds are not removed until such a time as the animal is ready to utilize them. That a large percentage of these buried stores are never again touched is a commonly accepted fact. That the trees suffer from this loss of seed seems incredible when one sees the vast number of seedlings that litter the forest floor; but that they ordinarily benefit from having the seeds planted for them is doubtful, since the cones are not usually buried at the proper depth or at a place suitable to encourage germination. These pockets are most frequently located under old logs or stumps, under living trees or under rocks—places where a germinating seed would never thrive. However, areas denuded by fires or lumbering are seeded from these buried stores through the efforts of squirrels from the adjacent forest that inadvertently drop a certain percentage of the seeds as they nip off the scales of the cones while perched on a stump, rock or log. Here the seeds are likely to find a favorable bed for germination.

During early September one pair of captive squirrels consumed the seed of 422 second year pine cones during one week of feeding. The only other food supplied them was apples of which they ate three during the same period. This number of cones represented approximately the total crop of two fifty-year-old trees during the

summer of 1925. In the natural state the squirrels at this time of year feed on large quantities of mushrooms, hazelnuts, and other foods, as well as on white pine seed. It seems then unlikely that a pair of squirrels working in the forest would at this time of year actually consume quite so large a quantity of pine seeds as did the captives, though they might cut an even larger number of cones for future use.

Late in August when squirrels in the spruce swamp were cutting off vast quantities of green cones the writer placed 90 such cones in a cage containing a pair of red squirrels. Though these individuals worked all of the seeds out from their scales they ate few or none of them, as was attested by the débris sifted from the cage.

Red squirrels within the forest were found feeding on butternuts, chestnuts, acorns of red oak, Scotch pine seeds and seeds of wild red cherry. It was reported, too, that they fed on the keys of the red maple in the spring. Elsewhere the author has found them feeding on the fruits of elm, apple, gray birch, and shag-bark hickory. It is presumed that the red squirrels of the Harvard Forest utilize these same food sources. Hornbeam, beech, white ash, white oak, and hawthorn are in all probability among the fruit trees of the squirrel though no definite records were obtained for these species.

The squirrels do not rely solely on trees for food but utilize as well the smaller plants. Until more is known of the importance of these various species composing forest undergrowth one cannot make any pretense of estimating the effect produced by the squirrels upon the forest trees through this source. Hazelnuts are used extensively by the red squirrels for autumn and winter food, and these animals are thus in keen competition with the chipmunks for this crop. Residents of the Petersham area rarely gather hazelnuts, so that the squirrel engenders no enmities in that direction. A pair of captive squirrels consumed 242 hazelnuts per day when fed no other food.

The late low blueberry (*Vaccinium vacillans*) which grows commonly in the forest was utilized to a considerable extent as current food supply. This species because of its low growth habit is not in demand by man, and the crop of berries is always far in excess of the demands made upon it by all other species, so that the squirrels take no more than a legitimate share.

Mushrooms of many species are used as food throughout the summer, and some of these are stored. The forms *Bolctus*, *Russula*, and *Amanita muscaria* were commonly eaten. No economic importance can be attached to this unless it be the indirect one of the animals having an additional source of food which will save the trees from some little further damage.



Fig. 208. Larch girdled by porcupine on the Harvard Forest. Photograph by A. C. Cline.



Fig. 209. Two mature hemlocks with all small twigs clipped by feeding porcupine. Photograph by A. C. Cline.



Fig. 210. The base of a Scotch pine completely girdled by mice, North Ashburnham, Massachusetts. July 18, 1925.



Fig. 211. A Scotch pine girdled by mice, which has sent up a new shoot from the base to replace the dead stem. September 10, 1925.

Gardens in the Petersham area are rarely molested, so far as could be learned.

The one remaining consideration relates to the squirrels as bird destroyers. This much discussed predatory habit is greatly overestimated by most people. That the squirrel does destroy eggs and nestlings of birds cannot be denied, but it appears to be an unusual thing. Seemingly only a few individuals possess the habit and they do not frequently follow such carnivorous inclinations. But one case of the kind came under the writer's personal observation. Here an immature red squirrel killed the nestlings of a black-throated green warbler, ate parts of the bodies and stored one in a pine as though for future use.

The case of the red squirrel is one calling for careful and unbiased judgment. A consideration of all its habits shows the squirrel to do as much good as harm in natural areas. Locally the species may at times become a pest, and then control measures must be adopted. In the Harvard Forest the only squirrel populations that need control are those in areas adjacent to plantations of larch, Scotch pine and Norway spruce. If during periods of heavy snowfall, the squirrels were to be shot, trapped, or, perhaps with greater economy, supplied with grain or scraps for food, the plantations might be unharmed. If abundant food were supplied during critical periods in the areas adjacent to plantations both trees and squirrels could possibly be kept alive. Trouble arises not in the relation of the squirrel to the native flora, but in introducing exotic species into an environment to which they have not been adapted by ages of natural selection.

Porcupine. The damage caused by this mammal at the present time appears to be limited to the barking of plantation trees of European larch and Scotch pine and to defoliation and barking of native hemlock. The only phase that is now of serious economic importance is the destruction of plantation trees. In two plantations of larch the trees injured exceeded twenty per cent of the number planted, and the number of these injured trees which died as the result of injury approximated three-fourths of the molested number. Scotch pine on the Forest has not yet been touched, but the seriousness of the damage in a nearby area warrants the expectation that the porcupines will soon become a pest to this species in the Harvard Forest, also. Such damage would appear to be controlled best locally during the winter months when porcupines can most easily be seen or tracked. The managers of the Forest, as a matter of

fact, have not found this an easy thing to do, for in 1923 twenty-one porcupines were killed around a small larch plantation without their numbers being accounted for completely. Damage to the trees continued practically undiminished in subsequent years.

It is not known that this species is of any benefit to the forest and for purposes of economy it would seem expedient to control their numbers by shooting and trapping during the winter months. Since the porcupine has but recently come into the region it is inconceivable that its extermination would disturb the balance of nature in this district.

Mice. Mice of one of the microtine species have done extensive damage to one Scotch pine plantation in the Forest. They have destroyed about twenty-five per cent of the trees in the stand.

The rôle that mice play in forestry is not sufficiently known. In times of over-population some species do enormous damage to forest and orchard trees. Even in years of ordinary populations bark-feeding may be locally serious, but in all probability this is usually offset by the good which they do.

The best known benefit derived by the forests from voles has recently been described by Graham ('28). He has shown that by feeding on the pupae of the larch sawfly, *Microtus* may prevent these insects from becoming epidemic.

The subject of the economic status of the voles is considered more at length in the preceding paper.

Deer. As previously stated, the deer damage is not so immediately serious as that caused by rodents. With a yearly open season on deer there has not been, nor is there likely to be, any overabundance of the species. At their present population they cannot be accused of damage great enough to offset the pleasure they afford to hunters or other recreation seekers in the Forest. The only practical control measure that might be undertaken against the deer would seem to be the fencing of young growth, but this to be effective might entail an expense that would be prohibitive.

THE INFLUENCE OF MAMMALS IN THE CULTIVATION OF VARIOUS SPECIES OF TREES

Larch. European larch has been used as a plantation tree in the Forest with unfortunate results. Squirrels, porcupines and the larch sawfly combine to make existence almost impossible for the species.

Six plantations of larch were surveyed in which the degree of damage by each species varied. A complete record was kept of all porcupine, squirrel and sawfly damage for one representative plantation. Of the trees in this stand, nine per cent were injured by porcupines (six per cent killed), sixty-three per cent were squirrel-cut and seventy per cent infested by sawfly larvae. A total of eighty per cent of the trees was damaged by one or more of these animals. The dead and dying constituted eleven per cent. The trees of this plantation were about twelve years old, and as the three enemies have but recently attacked them and shall probably continue to do so, the larches stand small chance of heavy survival.

Another plantation showed twenty per cent porcupine injury (sixteen per cent killed) and forty-one per cent red squirrel injury.

Still another had twenty-two per cent of the trees injured by porcupines (twelve per cent killed) and forty-three per cent damaged by red squirrels. Two other plantations with negligible porcupine damage showed every tree partly trimmed by red squirrels. Sawfly defoliation was found on sixty per cent of the trees in these stands. Damage to one of the plantations (P. H. VII, w) was so thorough that it is doubtful that the trees will live to a marketable age.

That they are to some extent protected by mice from further sawfly injury is probable, as Graham ('28) has shown that in the mid-western states *Microtus* feeds extensively on the pupae of this pest.

Scotch Pine. Scotch pine has been sporadically attacked in the region by mice and porcupines, each of which has made a serious inroad at the place of infestation. These two mammals while taking a toll of life among the trees have not in themselves ruined any one plantation beyond utilization. The red squirrel, though not actually killing trees has, however, in several stands so seriously deformed them through repeated feeding on the winter buds that commercially these trees are of but little value. Mouse damage is rare, though severe when it does occur. Porcupines probably feed continuously in a plantation but not in all plantations, while squirrels cause damage every winter in every plantation.

The plantation at North Ashburnham showed fifty-nine per cent of the trees injured by mice, half of which died. Porcupines had damaged thirty-two per cent of the trees, ten per cent of which subsequently died. Red squirrels had budded eighty-eight per cent of the whole. In all, mammals had killed thirty-two per cent of the trees and seriously injured about ninety per cent of all. Approximately eighty per cent of the trees planted could never be used for lumber, even though they might not be damaged further, which is hardly to be thought likely.

A plantation on the Harvard Forest (P. H. VIII, x) had fifty-one per cent of its trees girdled by mice, twenty-one per cent of all the trees being killed from this cause. In addition the stand had received damage to fifty per cent of its trees by red squirrels, though this injury was serious in relatively few cases. Two other plantations showed red squirrel damage to every tree, but had not been injured by any other mammal.

The serious effect of red squirrel injury is illustrated by a census of one hundred Scotch pines in which the number of times each had been robbed of its terminal bud was noted. Twelve had never had the leader injured, twenty-eight were injured but once, forty-two, twice; twelve, three times; five, four times; and one, five times. A total of eighty-eight were thus deformed.

The extent of cutting on a single tree was determined by selecting a representative individual and counting the number of lateral branches whose buds had been removed in each of the two preceding winters. During the winter 1924-1925 thirty-four per cent of the buds were removed, while in 1923-1924 thirty-two per cent were cut. As previously pointed out, this really does no injury to the tree as it only increases the leaf area, in contrast to the cutting of leaders which leads to serious consequences. A count of damaged leaders in this same plantation showed that at some time every tree had been attacked. The winter of 1923-1924 showed the greatest amount of damage, that of 1922-1923 the least, and that of 1924-1925 an amount intermediate between the others. It is said that the winter of 1923-1924 was the most severe of these three.

Norway Spruce. Red squirrels are the only mammals harming Norway spruce in the Harvard Forest. Their damage is usually not so serious as with other species of trees since defoliation is not great; and even though a leader is cut, ordinarily but a single lateral, close to the site of the original leader, grows upward. In time the tree straightens out and is not materially the worse for the loss of its



Fig. 212. A small group of Scotch pines killed by mice, North Ashburnham, Massachusetts. July 18, 1925.



Fig. 213. Pure growth white pine, Harvard Forest. August 10, 1925.

leader. Red squirrel injury coupled with that of the white pine weevil, which also kills the leader, must result in a considerable growth loss to the plantation as a whole, even though the individual tree does not show a very serious result.

Plantations which have escaped injury altogether were either too young to appear as trees above the snow or else were near a habitat which appeared to furnish enough food to keep the squirrels from feeding on spruce. Damage within a single plantation varied from one with no cuttings at all, to a stand in which every tree had been clipped and in which the terminals on ten per cent of the trees had at some time been cut.

Experimental Mixture. There is a one-acre plantation laid out in alternate rows of white pine, Scotch pine, western yellow pine, Norway spruce and Douglas fir. These trees were about eighteen years old when examined. They are closely planted and vary in height with the growth habits of the species. No trees except Norway spruce and Scotch pine had suffered injury by mammals. The damage to the spruce was not serious in any row, many trees not being affected at all. Scotch pines were already residence sites of squirrels and here the animals fed from both cones and buds. One single isolated row of Scotch pine showed no damage, and another, very light damage; but a strip three rows deep had some fifty per cent of the trees injured, and another, four rows wide, eighty per cent. Five other rows which were alternated with rows of white pine were too dense to allow a careful examination to be made, but about seventy-five per cent had been subjected to budding. The trees were in no case so seriously affected as were trees seen in pure stands.

General Considerations. The foregoing facts reveal several obvious errors in previous planting practice.

Small-sized plantations, particularly when placed near to or in a mature, though not old, forest, have been subject to thorough and constant injury by mammals feeding upon them. It would appear from this to be inadvisable to establish very small plantations within or near a forest from which mammals have easy access to all its parts, unless it be planted with a species known to be immune to such animal injury.

Exotic trees (Scotch pine, European larch and Norway spruce) have suffered more from the inroads of mammals than have indigenous forms. It would seem desirable, therefore, if market and

insect conditions are favorable, to use native species of trees where they are to be raised with a profit on the investment.

Pure stands have perhaps proved the gravest error for they have in many cases been subject to the attacks of insects and mammals to such an extent that the plantation is practically worthless, and the land on which they grow has in effect been idle. If alternate rows of different species are planted each species seems to enjoy a little more immunity than would otherwise have been its lot, and the plantation, even though the entire quota of one species be destroyed, may still thrive, and the development of a profitable stand may not be delayed.

That surrounding habitats play a most important rôle with mammals as well as with insects is illustrated by many facts. Norway spruce planted near one old and extensive forest of white pine and hardwood, the crown of which bore an abundant harvest and the underbrush of which contained a good growth of hazelnuts, was not subject to squirrel injury. This escape was seemingly because of a better balanced fauna and flora accompanying advanced age. Another spruce plantation, over four acres in area, was bordered on two sides by open fields, on the third by pasture with scattered pine occurring in it, and on the fourth by a mature growth of white pine and hardwood. The positions of injured and uninjured trees in the plantation were carefully mapped, the resulting plot showing clearly, by intensity of damage, an invasion of the plantation by red squirrels from the forest and from a stone wall leading out from the forest, along one border of the plantation. The corner farthest from the forest and fence showed by far the least damage, being in fact, practically untouched.

BIBLIOGRAPHY

- BAILEY, V.
1924. Breeding, Feeding and Other Life Habits of Meadow Mice (*Microtus*). Jour. Agric. Research, Vol. 27, No. 8, pp. 523-536.
- BALLOU, F. H.
1909. Protection of Fruit Trees from Rodents. Bull. Ohio. Agric. Exp. Sta., No. 208, pp. 53-70.
- BOWLES, J. H.
1920. The California Gray Squirrel An Enemy to the Douglas Fir. Amer. Forestry, Vol. 26, p. 26.
- FISHER, R. T.
1921. The Management of the Harvard Forest, 1909-1919. Harvard Forest Bull. 1, pp. 1-27.
1924. Catalog of Representative Operations on the Harvard Forest. Pp. 1-11. Athol, Mass.
- GRAHAM, S. A.
1928. The Influence of Small Mammals and Other Factors Upon the Larch Sawfly Survival. Jour. Economic Entomology, Vol. 21, No. 2, pp. 301-310.
- GRINNELL, J.
1924. Wild Animal Life as a Product and as a Necessity of National Forests. Jour. Forestry, Vol. 22, No. 8, pp. 837-845.
- HARTIG, R.
1895. Doppelringe als Folge von Spätfrost. Forstliche Naturwissenschaftliche Zeitung, Vol. 4, pp. 1-8. (Original not seen—R. T. H.)
- HATT, ROBERT T.
1929. The Red Squirrel: Its Life History and Habits, with Special Reference to the Adirondacks of New York and the Harvard Forest. Roosevelt Wild Life Annals, Vol. 2, No. 1, pp. 1-146.
- HOFMANN, J. V.
1920. The Establishment of a Douglas Fir Forest. Ecology, Vol. 1, pp. 49-53.
- HOSLEY, N. W.
1925. A Mystery of the Tree Tops. Amer. Forests and Forest Life, Vol. 31, pp. 455-457.
1928. Red Squirrel Damage of Coniferous Plantations and its Relation to Changing Food Habits. Ecology, Vol. 9, pp. 43-48.
- JACK, J. G.
1911. Trees and Other Woody Plants Found in the Harvard Forest, Petersham, Massachusetts. Bull. Harvard Forestry Club, Vol. 1, pp. 1-18.
- JOHNSON, C. E.
1918. Squirrels and Chipmunks in Autumn. Ottawa Nat., Vol. 32, No. 3, p. 54.
- LANTZ, D. E.
1906. Meadow Mice in Relation to Agriculture and Horticulture. U. S. Dept. Agric. Yrbk. for 1905, pp. 363-376.
1907. An Economic Study of the Field Mice (Genus *Microtus*). U. S. Dept. Agric., Biol. Survey Bull. No. 31, pp. 1-64.
1916. Cottontail Rabbits in Relation to Trees and Farm Crops. U. S. Dept. Agric., Farmers' Bull. No. 702, pp. 1-12.
1918. Field Mice as Farm and Orchard Pests. U. S. Dept. Agric., Farmers' Bull. No. 670, pp. 1-12.
- NICHOLS, J. T.
1927. Notes on the Food Habits of the Gray Squirrel. Jour. Mammalogy, Vol. 8, pp. 55-57.

- PEIRSON, H. B.
1924. Estimating Forest Insect Damage. Maine Forest Service Bull., No. 3, pp. 1-22.
- SHUFELDT, R. W.
1920. Four-footed Foresters—the Squirrels. Amer. Forestry, Vol. 26, pp. 37-44.
- SILVER, J.
1924. Mouse Control in Field and Orchard. U. S. Dept. Agric., Farmers' Bull. No. 1397, pp. 1-14.
- STONER, D.
1918. The Rodents of Iowa. Iowa Geol. Survey Bull., No. 5, pp. 1-172.
- THOREAU, H. D.
1906. The Succession of Forest Trees (An Address Read to the Middlesex Agricultural Society in Concord, September 1860). The Writings of Thoreau, Manuscript Ed., Vol. 5, pp. 184-204. Boston.

THE ROOSEVELT WILD LIFE MEMORIAL

As a State Memorial

The State of New York is the trustee of this wild life Memorial to Theodore Roosevelt. The New York State College of Forestry at Syracuse is a State institution supported solely by State funds, and the Roosevelt Wild Life Forest Experiment Station is a part of this institution. The Trustees are State officials. A legislative mandate instructed them as follows:

"To establish and conduct an experimental station to be known as 'Roosevelt Wild Life Forest Experiment Station,' in which there shall be maintained records of the results of the experiments and investigations made and research work accomplished; also a library of works, publications, papers and data having to do with wild life, together with means for practical illustration and demonstration, which library shall, at all reasonable hours, be open to the public." [Laws of New York, chapter 536. Became a law May 10, 1919.]

As a General Memorial

While this Memorial Station was founded by New York State, its functions are not limited solely to the State. The Trustees are further authorized to cooperate with other agencies, so that the work is by no means limited to the boundaries of the State or by State funds. Provision for this has been made by the law as follows:

"To enter into any contract necessary or appropriate for carrying out any of the purposes or objects of the College, including such as shall involve cooperation with any person, corporation or association or any department of the government of the State of New York or of the United States in laboratory, experimental, investigative or research work, and the acceptance from such persons, corporation, association, or department of the State or Federal government of gifts or contributions of money, expert service, labor, materials, apparatus, appliances or other property in connection therewith." [Laws of New York, chapter 42. Became a law March 7, 1918.]

By these laws the Empire State has made provision to conduct forest wild life research upon a comprehensive basis, and on a plan as broad as that approved by Theodore Roosevelt himself.

- ROOSEVELT WILD LIFE BULLETIN, Vol. 3, No. 1. February, 1925.
1. The Birds of the Yellowstone National Park.....Milton P. Skinner.
 2. Current Station Notes.....The Director and Editor.
- ROOSEVELT WILD LIFE BULLETIN, Vol. 3, No. 2. March, 1925.
1. The Muskrat in New York: Its Natural History and Economics.....
Dr. Charles E. Johnson.
 2. Current Station Notes.....The Director and Editor.
- ROOSEVELT WILD LIFE BULLETIN, Vol. 3, No. 3. September, 1926.
1. The Summer Birds of Central New York Marshes. Aretas A. Saunders.
 2. Additional Notes on the Summer Birds of Allegany State Park.....
Aretas A. Saunders.
 3. Current Station Notes.....The Director and Editor.
- ROOSEVELT WILD LIFE BULLETIN, Vol. 3, No. 4. October, 1926.
1. The Economic and Social Importance of Animals in Forestry, with
Special Reference to Wild Life.....Charles C. Adams.
 2. The Land—Economic Survey in Michigan.....R. A. Smith.
 3. Current Station Notes.....Charles C. Adams.
- ROOSEVELT WILD LIFE BULLETIN, Vol. 4, No. 1. October, 1926.
1. The Relation of Birds to Woodlots in New York State.....
Waldo L. McAtee.
 2. Current Station Notes.....Charles C. Adams.
- ROOSEVELT WILD LIFE BULLETIN, Vol. 4, No. 2. June, 1927.
1. The Predatory and Fur-bearing Animals of the Yellowstone National
ParkMilton P. Skinner.
 2. Current Station Notes.....Charles C. Adams.
- ROOSEVELT WILD LIFE BULLETIN, Vol. 4, No. 3. July, 1927.
1. A Trout Survey of Allegany State Park in 1922.....
William C. Kendall and Wilford A. Dence.
 2. A Preliminary Survey of the Fish Life of Allegany State Park in
1921Thomas L. Hankinson.
 3. Current Station Notes.....Charles C. Adams.
- ROOSEVELT WILD LIFE BULLETIN, Vol. 4, No. 4. July, 1927.
1. The Beaver in the Adirondacks: Its Economics and Natural History..
Charles E. Johnson.
- ROOSEVELT WILD LIFE BULLETIN, Vol. 5, No. 1. March, 1928.
1. A Preliminary Wild Life and Forest Survey of Southwestern Catta-
raugus Co., N. Y.....Victor H. Cahalane.
 2. A Preliminary Report on the Trout Streams of Southwestern Catta-
raugus Co., N. Y.....Wilford A. Dence.
- ROOSEVELT WILD LIFE BULLETIN, Vol. 5, No. 2. February, 1929.
1. The Fishes of the Cranberry Lake Region.....
W. C. Kendall and W. A. Dence.
 2. The Story of King's Pond.....F. A. Lucas.
 3. Its Fish Cultural Significance.....W. C. Kendall.
- ROOSEVELT WILD LIFE BULLETIN, Vol. 5, No. 3. September, 1929.
1. The Summer Birds of the Northern Adirondack Mountains.....
Aretas A. Saunders.
 2. The Summer Birds of the Adirondacks in Franklin County, N. Y.....
Theodore Roosevelt, Jr., and H. D. Minot.

(Reprinted: original date of publication, 1877.)

